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AN ANNOTATED BIBLIOGRAPHY ON THE BIOLOGY OF PACIFIC TUNAS

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CONTENTS

	Page
Introduction	1
Annotated bibliography	3
Abbreviations used	25
Index by subjects	28

AN ANNOTATED BIBLIOGRAPHY ON THE BIOLOGY OF PACIFIC TUNAS

By Bell M. Shimada, *Fishery Research Biologist*

Studies were begun in 1948 by the Pacific Oceanic Fishery Investigations of the U. S. Fish and Wildlife Service to gather fundamental data on the life histories, ecology, and behavior of the various species of Pacific tunas. Early in the planning of the research program conducted from the Hawaiian Islands, it was recognized that review and systematic compilation of the literature on these subjects were essential to the effective guidance of the projected research. The principal reference work available was the bibliography of the tunas prepared some 20 years ago by Genevieve Corwin (see Corwin 1930, in the Bibliography, p. 5). To meet the needs of the workers in the Investigations, and to assist tuna researchers in general, the preparation of this bibliography was undertaken.

The bibliography deals chiefly with the black skipjacks or little tunnies (*Euthynnus alletteratus*, *E. lineatus*, and *E. yaito*), the oceanic or common skipjack (*Katsuwonus pelamis*), the albacore (*Thunnus germo*), the bluefin or black tunas (*Thunnus maccoyi*, *T. orientalis*, and *T. thynnus*), the big-eyed tunas (*Parathunnus mebachi* and *P. sibi*), the yellowfin tuna (*Neothunnus macropterus*), and the frigate mackerels of the genus *Auxis*. Synonymous and related species reported from the Pacific Ocean are included. Waters contiguous to the Indo-Australian Archipelago have been considered as a part of the Pacific Ocean proper, inasmuch as many of the important studies of tuna species occurring in the Pacific Ocean were based on data gathered in that region.

In the review of the literature, some preliminary work was done at Stanford University, Palo Alto, and at the California Academy of Sciences, San Francisco, California. The libraries of the Bernice Pauahi Bishop Museum, the University of Hawaii, and the Territorial Board of Agriculture and Forestry in Honolulu, and private collections of staff members of the Investigations were particularly productive of material. The Japanese references were gathered by a reconnaissance team in Japan from November 1948 to July 1949 investigating the results of Japanese tuna research. Search of private and public libraries in and about Tokyo supplied much material that has not hitherto been generally available outside Japan. Some references found in Corwin's bibliography could not be examined at first hand; these are included here, as given by Corwin, with a notation to show their source.

The general style used by Corwin has been followed in cataloging and annotating the material. The arrangement of the references is by authors listed alphabetically. Entry is made only under the senior author's name if there is more than one author; the abbreviation "et al." is used with the senior author's name to show collaboration of more than three authors. Each author's works are listed chronologically by year of publication, and those published in the same year are given in alphabetical sequence. Generally, pagination is given only for the parts of the publication falling within the scope of the bibliography.

Appropriate notations in the bibliography distinguish those papers published only in Japanese, those published in Japan but written in English, and those published in Japanese with an English abstract. Translations were made of Japanese titles when English equivalents were not given.

Brief annotations of the publications are included except for those that could not be consulted and for those whose titles give a clear indication of the contents. The scientific nomenclature used by each author is followed in the annotations; appropriate cross references to synonymous names regarded as having priority appear in the Index. Where both vernacular and scientific names of the tuna were given, the scientific nomenclature is retained.

The preparation of the Index presented considerable difficulty owing to the confused state of the

taxonomy of the various species of tuna. As the relationships of the tuna species of the Pacific, and for that matter the world in general, have not been clearly defined, specific names of questionable validity have been arbitrarily indexed as separate entries. For example, *Neothunnus itosibi* is regarded by some workers as a form distinct from *Neothunnus macropterus*, while others consider the two to be synonymous. References to *Neothunnus itosibi* and *Neothunnus macropterus*, therefore, have been treated separately. Synonyms which are generally accepted as applying to one given species, such as *Euthynnus pelamis* for *Katsuwonus pelamis*, have been indexed under the name which is believed to have priority, with appropriate cross reference under the synonymous name. The same procedure was used in indexing names which differ slightly in spelling. Again, it should be pointed out that the indexing of these scientific names is to a large degree arbitrary, and is not an attempt to clarify the systematics of the tunas.

A list of abbreviations of the various publications cited and of the English translations of titles of Japanese periodicals as used in the bibliography is included.

Acknowledgment is made of the valuable assistance and advice given the author by various individuals and organizations. Especially is credit due the Fisheries Division, Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers, under W. C. Herrington, Drs. K. Kuronuma and Y. Hiyama, and other Japanese scientists, and Dr. J. G. F. Hardenburg of Batavia, Java, for their generous cooperation. The author is also indebted to the library staffs of Stanford University, the California Academy of Sciences, University of Hawaii, and the Bernice Pauahi Bishop Museum, and to Vernon Brock of the Division of Fish and Game, Board of Agriculture and Forestry, Territory of Hawaii, and staff members of the Pacific Oceanic Fishery Investigations, who contributed materially to the preparation of this bibliography.

ANNOTATED BIBLIOGRAPHY

Explanation of symbols

[C] = references listed by Corwin (see Corwin 1930, p. 5) that could not be verified.
[J] = published in Japanese only.
[JE] = published in Japan but written in English.
[Je] = written in Japanese with English abstract.
[P] = accession to the library of the Pacific Oceanic Fishery Investigations.

[For an explanation of the abbreviation see list, p. 25]

ABE, TOKIHARU.

1939. A list of the fishes of the Palao Islands. Palao Trop. Biol. Sta. Studies, No. 4, p. 567. [JE] [P]
Germo macropterus, Katsuwonus pelamys, Thunnus thynnus: recorded; distribution.

AIKAWA, HIROAKI.

1933. Fishery conditions on the Pacific Coast for skipjack, tuna, and sauries. Proc. Sci. Fish. Assoc., vol. 5, No. 4, pp. 354–369. [J] [P]
Albacore, big-eyed tuna, black tuna, skipjack, yellowfin tuna: fishing conditions correlated with surface water temperature.

1937. Notes on the shoal of bonito along the Pacific Coast of Japan. Bull. Japanese Soc. Sci. Fish., vol. 6, No. 1, pp. 13–21. [Je] [P]
Age analysis and size composition of skipjack catches; stock and population relationships; use of condition factor in separating migratory and nonmigratory fish.

AIKAWA, HIROAKI, and MASAO KATO.

1938. Age determination of fish. I. Bull. Japanese Soc. Sci. Fish., vol. 7, No. 2, pp. 79–88. [Je] [P]
Germo germo, Katsuwonus vagans, Neothunnus macropterus, Thunnus orientalis: age analysis using vertebrae; age composition of commercial catch; calculated length and weight groups; body condition; growth rate; morphometric data.

ANONYMOUS.

1938. Status of the investigation of tuna longline fishing grounds in the South China Sea. Formosa Fish. Mag., No. 279, pp. 10–19. [J]
Albacore, yellowfin tuna: body temperatures; distribution; length-weight data; sexual maturity; stomach contents; figured.

1939. Marked fish. Semi-Ann. Rpt. Oceanogr. Invest., No. 65, p. 137. [J]
Skipjack: Japan; release records of tagged fish.

1941. Pacific skipjack indigenous to Sulu Sea. South Sea Fish., vol. 7, No. 5, p. 55. [J] [P]
Distributional note.

ASANO, NAGAO.

1939. Food of the albacore, *Germo germo* (Lacépède). South Sea Fish. News, vol. 3, No. 7, pp. 10–11. [J] [P]
South Seas; stomach contents; *Auxis* sp. recorded as food.

BAN, YOSHINORI.

1941. Search for southern tuna fishing grounds. South Sea Fish., vol. 7, No. 9, pp. 10–21. [J] [P]
Yellowfin tuna: South Seas; fishing conditions correlated with oceanography; stomach contents: age analysis; sexual maturity.

BARNHART, PERCY.

1936. Marine fishes of Southern California. Univ. California Press, Berkeley, pp. 36–37.
Auxis thazard, Katsuwonus pelamis, Germo alalunga, Neothunnus macropterus, Thunnus thynnus: description; distribution; English common names; figures.

BENNETT, FREDERICK DEBELL.

1840. Narrative of a whaling voyage around the globe, from the year 1833 to 1836. Vol. 2, pp. 278–282. London.
Scomber germo: description; anatomy of reproductive system; food; enemies. *Scomber pelamys:* description; parasites.

BERG, LEO S.

1947. Classification of fishes both recent and fossil. J. W. Edwards Co., Ann Arbor, pp. 491–492.
Anatomy and classification of Thunniformes (Plecostei).

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1844. Bijdragen tot de geneeskundige topographie van Batavia. Generisch overzicht der fauna. Nat. Geneesk. Arch. Neerland's Indië, vol. 1, p. 553.
Thynnus: recorded.

1845. Bijdragen tot de geneeskundige topographie van Batavia. Generisch overzicht der Fauna. Nat. Geneesk. Arch. Neerland's Indië, vol. 2, p. 516.
Auxis taso: recorded.

1850. Bijdrage tot de kennis der ichthyologische fauna van Midden-en Oost-Java, met beschrijving van eenige nieuwe species. Verh. Batavia Genoot. Kunst. Wetens., vol. 23, p. 8.
Auxis taso: recorded.

1852. Bijdrage tot de kennis der makreelachtige visschen van den Soenda-Molukschen Archipel. Verh. Batavia Genoot. Kunst. Wetens., vol. 24, pp. 36–37, 89.
Thynnus macropterus, T. thunnina, and *T. tonggol:* recorded from Dutch East Indies; description and synonymy of *T. tonggol.*

Bleeker, Pieter—Continued

1854. Faunae ichthyologicae japonicae species novae. Nat. Tijdschr. Nederlandsch-Indie, vol. 6, pp. 408–409.
Auxis tapeinosoma: recorded and described.

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Auxis thynnoides: recorded; description; compared with *A. tapeinosoma*, *A. taso*, and *A. vulgaris*.

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Thynnus pelamys: recorded; description; synonymy.

1857. Nieuwe nalezingen op de ichthyologie van Japan. Verh. Batavia Genoot. Kunst. Wetens., vol. 26, p. 98.
Auxis tapeinosoma: recorded.

1860a. Achtste bijdrage tot de kennis der vischfauna van Sumatra. Vissehen van Benkoelen, Priaman, Tandjong, Palembang, en Djambi. Act. Soc. Sci. Indo-Neerlandicae, vol. 8, p. 29.
Thynnus pelamys, T. thunnina: recorded from the Dutch East Indies.

1860b. Dertiende bijdrage tot de kennis der vischfauna van Celebes. Visschen van Bonthain, Badjoa, Sindjai, Lagoesi en Pompenoea. Act. Soc. Sci. Indo-Neerlandicae, vol. 8, p. 38. [C]
Thunnus thunnina: recorded from Dutch East Indies.

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Thynnus affinis: recorded from Dutch East Indies.

1861b. Mededeeling omtrent vischsoorten, nieuw voor de kennis der fauna van Singapoera. Versl. Akad. Amsterdam, vol. 12, p. 52. [C]
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1865a. Énumération des espèces de poissons actuellement connues de l'île d'Amboine. Nederlandsch Tijdschr. Dierk., vol. 2, p. 285.
Auxis thynnoides, Pelamys macropterus, P. pelamys, P. thunnina: recorded.

1865b. Sixième notice sur la faune ichthyologique de Siam. Nederlandsch Tijdschr. Dierk., vol. 2, p. 173. [C]
Thynnus thunnina: recorded.

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Katsuwonus pelamis: length-weight data and relationship; length frequencies of *Neothunnus macropterus;* lengths of *Euthynnus yaito.*

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Thunnus thynnus: recorded.

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Age and size composition; growth; spawning; sex ratio; length-frequency data; population analysis.

1949. A preliminary report on *Parathunnus sibi* in Hawaiian waters and a key to the tunas and tuna-like fishes of Hawaii. Pacific Sci., vol. 3, No. 3, pp. 271–277.
P. sibi: description; morphometric data; feeding habits. *Auxis thazard, Euthynnus yaito, Germo alalunga, Katsuwonus pelamis, Kishinoella rara, Neothunnus macropterus, Parathunnus sibi, Thunnus orientalis, T. thynnus:* key.

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1932b. Poissons des campagnes du "de Lanessan" (1925–1929). Trav. Inst. Oceanogr. Indochine, 4e Mém., pp. 113–115.

Euthynnus yaito: synonymy; distribution; description; Indo-Chinese common names; figure of specimen and scales.

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Japan; albacore and skipjack fishing conditions correlated with water temperature.

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Japan; skipjack catch correlated with water temperature.

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Japan; skipjack catch correlated with water temperature.

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Population studies based on comparisons of body proportions, counts of meristic characters, and sexual maturity.

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1863. On new genera and species of Californian fishes. Proc. California Acad. Sci., vol. 3, pp. 75–77.

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CUVIER, GEORGES, and ACHILLES VALENCIENNES.

1831. Histoire naturelle des poissons. Vol. 8, pp. 85, 96, 107. Paris.

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DEJONG, J. K.

1940. A preliminary investigation of the spawning habits of some fishes of the Java Sea. Treubia, vol. 17, No. 4, pp. 325–326.

Euthynnus allitteratus: frequencies of egg diameter measurements; resorption of eggs noted.

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1931. Fish eggs and larvae from the Java Sea. Treubia, vol. 13, Nos. 3–4, pp. 407–409.

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1940. Tuna fishing in Southern Mindanao. Philippine Jour. Sci., vol. 73, No. 4, pp. 423–435.

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1949b. Observations on juvenile oceanic skipjack (*Katsuwonus pelamis*) from Hawaiian waters and sierra mackerel from the Eastern Pacific. U. S. Fish and Wildlife Serv. Fish. Bull., vol. 51, No. 48, pp. 245–250.

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1892. The fishes of San Diego, California. Proc. U. S. Natl. Mus., vol. 15, No. 897, pp. 130, 147.

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Stomach contents of *Neothunnus macropterus.*

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1931. Northern oceanographic conditions and skipjack fishing. Prog. Rpt. Formosa Govt.-Gen. Fish. Expt. Sta. for 1929, Oceanogr. Sec., pp. 28–30. [J] [P]

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Germo germon: figured.

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KAGOSHIMA PREFECTURAL FISHERIES EXPERIMENT STATION.

1925. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1923, pp. 1–37. [J] [P]

Ryukyu Islands; skipjack fishing conditions correlated with water temperature; length-weight, girth data.

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1927b. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1925, pp. 1–38. [J] [P]

Ryukyu Islands; skipjack fishing conditions correlated with water temperature and currents; length-weight and girth data; records and descriptions of scombroid juveniles (also reported in Kishinouye 1926).

1928a. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1926, pp. 1–22. [J] [P]

Ryukyu Islands; skipjack catch correlated with water temperature and currents; length-weight and girth data; release records of tagged fish.

1928b. Experimental longline fishing for tuna. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1926, pp. 22–37. [J] [P]

Albacore, big-eyed tuna, black tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

KAGOSHIMA PREFECTURAL FISHERIES EXPERIMENT STATION—Continued

1929a. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1927, pp. 1–20. [J] [P]

Ryukyu Islands; skipjack catch correlated with water temperature; length-weight and girth data.

1929b. Experimental longline fishing for tuna. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1927, pp. 20–34. [J] [P]

Big-eyed tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

1930a. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1928, pp. 1–18. [J] [P]

Ryukyu Islands; skipjack catch correlated with water temperature.

1930b. Experimental longline fishing for tuna. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1928, pp. 18–31. [J] [P]

Albacore, big-eyed tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

1930c. Experimental fishing by small motor vessels: Experimental longline fishing for albacore. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1928, pp. 54–60. [J] [P]

Albacore, big-eyed tuna, black tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

1931a. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1929, pp. 1–16. [J] [P]

Ryukyu Islands; skipjack catch correlated with water temperature.

1931b. Experimental longline fishing for tuna. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1929, pp. 16–30. [J] [P]

Albacore, big-eyed tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

1932a. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1930, pp. 1–20. [J] [P]

Ryukyu Islands; skipjack fishing conditions correlated with water temperature.

1932b. Experimental longline fishing for tuna. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1930, pp. 21–28. [J] [P]

Albacore, big-eyed tuna, black tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

1932c. Experimental longline fishing for albacore and pole and line fishing for mackerel. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1930, pp. 54–59. [J] [P]

Ryukyu Islands; albacore catch correlated with water temperature.

KAGOSHIMA PREFECTURAL FISHERIES EXPERIMENT STATION—Continued

1933a. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1931, pp. 1–16. [J] [P]

Ryukyu Islands, Philippine region; skipjack fishing conditions correlated with water temperature.

1933b. Experimental longline fishing for tuna. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1931, pp. 16–23. [J] [P]

Albacore, big-eyed tuna, yellowfin tuna: Ryukyu Islands; catches correlated with water temperature.

1935. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1933, pp. 1–12. [J] [P]

Ryukyu Islands; skipjack fishing conditions correlated with water temperature.

1936a. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1934, pp. 1–16. [J] [P]

Ryukyu Islands; skipjack fishing conditions correlated with water temperature; length-weight data.

1936b. Investigation of the migration of important fishes. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1934, pp. 86–87. [J] [P]

Ryukyu Islands; release records of tagged skipjack.

1937. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1935, pp. 1–8. [J] [P]

Ryukyu Islands; skipjack catch correlated with water temperature; length-weight data; size composition of catch.

1938a. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1936, pp. 1–4. [J] [P]

Ryukyu Islands; skipjack length-weight data.

1938b. Investigation of the migration of important fishes. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1936, p. 89. [J] [P]

Ryukyu Islands; release records of tagged skipjack.

1939a. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1937, pp. 1–3. [J] [P]

Ryukyu Islands; skipjack length-weight data.

1939b. Investigation of the migration of important fishes. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1937, p. 69. [J] [P]

Ryukyu Islands; release records of tagged skipjack.

1940a. Experimental skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1938, pp. 1–3. [J] [P]

Ryukyu Islands; skipjack length-weight data.

1940b. Investigation of the migration of important fishes. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1938, p. 43. [J] [P]

Ryukyu Islands; release records of tagged skipjack.

KAGOSHIMA PREFECTURAL FISHERIES EXPERIMENT STATION—Continued

1941. Investigation of skipjack fishing. Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta. for 1939, pp. 1–3. [J] [P]

Ryukyu Islands; skipjack length-weight data.

KANAMURA, MASAMI, and KAKUJI IMAIZUMI.

1935. Report on experimental fishing by the Shonan Maru in 1935: Report of experimental longline fishing for tuna in eastern Formosan waters. Formosa Govt.-Gen. Fish. Expt. Sta. Publ., No. 3, pp. 165–202. [J] [P]

Big-eyed tuna, yellowfin tuna: length-weight data; body temperatures; sexual maturity; catch per unit of effort; fishing conditions in relation to oceanography and weather; distribution.

KANAMURA, MASAMI, and HARUO YAZAKI.

1940a. Report on experimental fishing by the Shonan Maru in 1937: Investigation of tuna longline fishing grounds in the East Philippine Sea. Formosa Govt.-Gen. Fish. Expt. Sta. Publ., No. 21, pp. 1–65. [J] [P]

Albacore, big-eyed tuna, skipjack, yeltowfin tuna: catch per unit of effort; distribution of yellowfin, big-eyed tuna, and skipjack; yellowfin tuna: stomach contents; body temperature and relation to water temperature; length-weight data; body condition; age analysis; sexual maturity; fishing conditions in relation to oceanography and weather.

1940b. Report of the investigation of fishing grounds by the Shonan Maru in 1937: Investigation of tuna longline fishing grounds in the South China Sea. Formosa Govt.-Gen. Fish. Expt. Sta. Publ., No. 21, pp. 67–117. [J] [P]

Albacore, skipjack, yellowfin tuna: distribution; catch per unit of effort; fishing conditions in relation to oceanography and weather; albacore, yellowfin tuna: stomach contents; body temperature; length-weight data; body condition; age analysis; sexual maturity.

KATO, GENJI.

1940. An account of longline fishing for tuna. South Sea Fish. News, vol. 4, No. 7, pp. 8–10. [J] [P]

Sexual maturity of yellowfin tuna noted.

KAWAMURA, HYŌZŌ.

1939. Observations on oceanography and fishing conditions in Palau waters. South Sea Fish. News, vol. 3, No. 1, pp. 2–6. [J] [P]

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KIDA, TAKEO.

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Thynnus thynnus: fishing conditions correlated with water temperature; size composition of schools; habits.

KIMURA, KINOSUKE.

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Neothunnus macropterus, Thunnus orientalis: growth rates determined from size groups.

1935. Statistical analysis of the catch by keddle nets, along the coast of Surugu Bay. Rec. Oceanogr. Works, vol. 7, No. 1, pp. 1–36. [JE]

Growth of *Neothunnus macropterus;* age and size groups of *Thunnus orientalis.*

1941. Skipjack fishing. Fish. Technol. Lect. Ser., No. 4, 36 pp. [J]

Pacific Ocean; distribution; migration; catch correlated with water temperature; age and size composition of commercial catches.

1942a. Tuna and spearfish fishing conditions. Fish. Technol. Lect. Ser., No. 5, 122 pp. [J]

Albacore, big-eyed tuna, yellowfin tuna: Japan, Indo-Pacific region, South Seas; fishing conditions correlated with water temperature; age and size composition of albacore and yellowfin tuna.

1942b. Oceanic resources: Offshore fisheries. Sci. Sea, vol. 2, No. 3, pp. 142–147. [J] [P]

Albacore, black tuna, skipjack: Pacific Ocean; distribution; migration; distribution of big-eyed tuna and yellowfin tuna.

1949. Atlas of skipjack fishing grounds—with data on the albacore grounds. Kuroshio Publ. Co., Tokyo, 44 pp. [J]

Japan; catches of albacore and skipjack correlated with surface water temperature.

KIMURA, KINOSUKE, and KAZUMI ISHII.

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Catches of yellowfin tuna correlated with water temperature.

KISHINOUYE, KAMAKICHI.

1895. Food of tunas and bonitos. Zool. Mag., vol. 7, p. 111. [J]

1915a. Studies on the mackerels, cybiids, and tunas. Proc. Sci. Fish. Assoc., vol. 1, No. 1, pp. 1–24. [J] [P]

Auxis hira n. sp., *A. maru* n. sp., *Euthynnus yaito* n. sp., *Katsuwonus pelamys* n. sp., *Thunnus alalunga, T. macropterus, T. mebachi* n. sp., *T. orientalis, T. rarus* n. sp.: internal anatomy; classification; description; distribution; keys; Japanese common names; figures; spawning of *T. orientalis* and *A. maru;* food and habits of tunas in general.

KISHINOUYE, KAMAKICHI—Continued

1915b. Anatomical aspects of dark muscle. Proc. Sci. Fish. Assoc., vol. 1, No. 2, pp. 128–136. [J] [P]
Albacore, big-eyed tuna, black skipjack, black tuna, frigate mackerel, *Neothunnus rarus*, skipjack, yellowfin tuna: anatomy and vascular system of lateral musculature described; figured in part for all except big-eyed tuna and *N. rarus*.

1917a. A new order of the Teleostomi. Proc. Sci. Fish. Assoc., vol. 2, No. 2, pp. 1–4. [J] [P]
Classification; description of internal anatomy of order Plecostei and families Thunnidae and Katsuwonidae.

1917b. The food of tunas. Proc. Sci. Fish. Assoc., vol. 2, No. 1, pp. 106–108. [J] [P]
Albacore, big-eyed tuna, skipjack, yellowfin tuna: stomach contents; juvenile albacore, big-eyed tuna, skipjack, and *Auxis maru* recorded from stomachs of adults.

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Blood content of dark lateral muscle of big-eyed tuna and skipjack compared.

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Evolution of various tuna species based on internal anatomy; vascular system and anatomy of lateral musculature of Thunnidae and Katsuwonidae; and vascular plexuses of albacore, big-eyed tuna, black skipjack, black tuna, frigate mackerel, skipjack, and yellowfin tuna figured.

1919b. The larval and juvenile stages of the Plecostei. Proc. Sci. Fish. Assoc., vol. 3, No. 2, pp. 49–53. [J] [P]
Black skipjack, black tuna, skipjack: western Pacific; juveniles recorded and described; markings of young Scombroid fishes mentioned; Lütken's "albacore" juveniles and Günther's "black skipjack" juvenile described and figured.

1919c. Btack skipjack from Mexico. Proc. Sci. Fish. Assoc., vol. 3, No. 2, p. 113. [J] [P]
Euthynnus lineatus: Mexico; recorded and described as a new species.

1921. Tunas of the American coast. Proc. Sci. Fish. Assoc., vol. 3, No. 3, p. 239. [J] [P]
Anatomical differences between American bluefin tuna and Japanese black tuna noted.

1922a. Air bladders of Thunnidae. Proc. Sci. Fish. Assoc., vol. 3, No. 4, p. 304. [J] [P]
Albacore, big-eyed tuna, yellowfin tuna: air-bladders described; recorded and described for black tuna.

1922b. Carangid-like markings of skipjack. Proc. Sci. Fish. Assoc., vol. 3, No. 4, pp. 304–305. [J] [P]
Unusual markings on one specimen recorded and described.

1922c. Black skipjack also found in Japan Sea. Proc. Sci. Fish. Assoc., vol. 3, No. 4, p. 305. [J] [P]
Distribution record.

KISHINOUYE, KAMAKICHI—Continued

1923. Contributions to the comparative study of the so-called Scombroid fishes. Jour. Coll. Agr., Imp. Univ. Tokyo, vol. 8, No. 3, pp. 293–475. [P]
Auxis hira, A. maru, Euthynnus lineatus, E. yaito, Katsuwonus pelamis, Neothunnus macropterus, N. rarus, Parathunnus mebachi, Thunnus germo, T. orientalis: anatomy; bibliography; classification; description; distribution; figures; food; habits; keys; Japanese common names; synonymy; growth of *N. macropterus, T. germo, T. orientalis;* enemies of *T. orientalis;* migration of *K. pelamis, T. germo, T. orientalis;* parasites of *E. yaito, K. pelamis, N. macropterus, P. mebachi;* spawning of *E. yaito, K. pelamis, N. macropterus, T. orientalis;* young of *A. maru, E. yaito, K. pelamis, T. germo, T. orientalis.*

1924. Observations on skipjack fishing grounds. Proc. Sci. Fish. Assoc., vol. 4, No. 2, pp. 87–92. [J] [P]
Auxis maru, Euthynnus yaito, Katsuwonus pelamis, ?Neothunnus macropterus: Ryukyu Islands; records and descriptions of juveniles.

1926. An outline of studies of the Plecostei (tuna and skipjack) in 1925. Proc. Sci. Fish. Assoc., vol. 4, No. 3, pp. 125–137. [J] [P]
Auxis sp., *Katsuwonus pelamis, ?Neothunnus macropterus, ?Parathunnus mebachi:* Ryukyu Islands; juveniles recorded, described, and figured.

KITAHARA, T.

1897. Scombridae of Japan. Jour. Imp. Fish. Bur., Tokyo, vol. 6, pp. 1–3. [C]
Thynnus germo, T. macropterus, T. pelamys, T. sibi, T. thunnina, T. thynnus: figures.

KŌCHI PREFECTURAL FISHERIES EXPERIMENT STATION.

1923a. Oceanographic observations and search for skipjack fishing grounds. Prog. Rpt. Kōchi Pref. Fish. Expt. Sta. for 1921, pp. 1–4. [J] [P]
Japan; skipjack fishing conditions correlated with oceanographic factors.

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Albacore, big-eyed tuna, yellowfin tuna: Japan; migration; vertical distribution.

1924. Oceanographic observations and search for tuna fishing grounds. Prog. Rpt. Kōchi Pref. Fish. Expt. Sta. for 1922, pp. 39–49. [J] [P]
Albacore, big-eyed tuna, black tuna, yellowfin tuna: Japan; migration; vertical distribution.

KODAMA, MASAHARU, KIYOSHI IIZUKA, and TOSHI HARADA.

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Skipjack and tuna examined.

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Ryukyu Islands; skipjack fishing conditions correlated with water temperature.

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Katsuwonus vagans, Neothunnus macropterus, Parathunnus mebachi: distribution; English and Japanese common names; figures; Dutch and Malayan common names of *N. macropterus* and *P. mebachi.*

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Stomach contents of *Germo germo* noted.

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Thynnus vagans: description; distribution; figured.

LORD, CLIVE.

1927. A list of the fishes of Tasmania. Jour. Pan-Pacific Res. Inst., vol. 2, No. 4, p. 15.

Auxis thazard, Thunnus maccoyi: listed.

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MACLEAY, WILLIAM.

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Thynnus affinis, T. maccoyi, T. pelamys: description; distribution.

MANTER, HAROLD W.

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Gymnosarda alletterata and *G. pelamis* listed as hosts.

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Katsuwonus pelamis: Marshall Islands; records and descriptions of juveniles; ova measurements. *K. pelamis, Neothunnus macropterus:* spawning; length, sex, maturity data.

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Auxis ramsayi, A. thazard, Euthynnus alletterata, E. pelamis, Thunnus germo, T. maccoyi: listed; synonymy; key; figures of *A. thazard, E. pelamis*, and *T. maccoyi.*

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Auxis thazard, Germo atalunga, Gymnosarda alletterata, G. pelamis, Thunnus thynnus: description; distribution; key; synonymy.

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Germo alalunga, Thunnus thunnus: recorded.

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Japan; skipjack fishing conditions correlated with water temperatures and specific gravity.

1930b. Skipjack fishing and oceanographic conditions. Prog. Rpt. Mie Pref. Fish. Expt. Sta. for 1927, pp. 15–17. [J] [P]
Japan; skipjack fishing conditions correlated with water temperature and specific gravity.

1930c. Investigation of tuna fishing grounds and guidance in fishing. Prog. Rpt. Mie Pref. Fish. Expt. Sta. for 1927, pp. 18–33. [J] [P]
Albacore, big-eyed tuna, black tuna, yellowfin tuna: Japan; fishing conditions correlated with water temperature and specific gravity.

1930d. Investigation of skipjack fishing grounds and guidance in fishing. Prog. Rpt. Mie Pref. Fish. Expt. Sta. for 1928, pp. 1–18. [J] [P]
Japan; skipjack fishing conditions correlated with water temperature and specific gravity.

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Albacore, big-eyed tuna, black tuna, yellowfin tuna: Japan; fishing conditions correlated with water temperature and specific gravity.

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Frigate mackerel, skipjack, *Thunnus orientalis*, yellowfin tuna: melanophorhormone content of pituitary glands tabulated; proportional weights of various parts of *T. orientalis* brain; brain of yellowfin tuna figured.

Mine, Tatsuzō, and Satoru Iehisa.

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Size composition of commercial catch.

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Big-eyed tuna, black tuna, skipjack, yellowfin tuna: chemical analysis of liver and liver oil.

Miyama, Yoshimichi, Kuman Saruya, and Takayoshi Hasegawa.

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Thunnus macropterus: South Seas; chemical analysis of various body parts; length-weight data, sex, and stomach contents of specimens recorded.

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Albacore, big-eyed tuna, black skipjack, black tuna, skipjack: chemical analyses of flesh and dark muscle.

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Auxis thazard, Thunnus orientalis: listed.

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Analyses of stomach contents; length-weight data.

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Description and figure of mature egg; gonads figured; distribution; sexual maturity; spawning areas and season.

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1940b. A note on the fisheries condition of "katuo" as a function of several oceanographic factors. Bull. Japanese Soc. Sci. Fish., vol. 9, No. 4, pp. 145–148. [Je] [P]

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ABBREVIATIONS USED

A. Hancock Pacific Exped.—Allan Hancock Pacific Expeditions. Los Angeles.

Acad. Nat. Sci. Phila., Monogr.—Academy of Natural Sciences of Philadelphia, Monographs. Philadelphia.

Act. Soc. Sci. Indo-Neerlandicae—Acta Societatis Scientarium Indo-Neerlandicae. Batavia.

Ann. and Mag. Nat. Hist.—The Annals and Magazine of Natural History. London.

Ann. New York Acad. Sci.—Annals of the New York Academy of Sciences. New York.

Ann. Rpt. Laguna Mar. Lab.—Annual Report of the Laguna Marine Laboratory. Claremont, California.

Annot. Zool. Jap.—Annotationes Zoologicae Japonenses. Tokyo.

Arch. Neêrlandaises Sci. Nat.—Archives Neêrlandaises des Sciences Exactes et Naturelles. Haarlem.

Australian Zool.—The Australian Zoologist. Sydney.

Bernice P. Bishop Mus. Occas. Papers—Bernice Pauahi Bishop Museum. Occasional Papers. Honolulu.

Biblio. Nederlandsch Indische Nat. Ver.—Bibliotheek van de Nederlandsch Indische Natuurhistorische Vereeniging. Batavia.

Biol. Bull. St. John's Univ.—Biological Bulletin of St. John's University. Shanghai.

Bull. American Mus. Nat. Hist.—Bulletin of the American Museum of Natural History. New York.

Bull. Bernice P. Bishop Mus.—Bulletin. Bernice Pauahi Bishop Museum. Honolulu.

Bull. Biogeog. Soc. Japan—Bulletin of the Biogeographical Society of Japan. Tokyo.

Bull. U. S. Bur. Fish.—Bulletin of the Bureau of Fisheries. United States Department of Commerce and Labor. Washington.

Bull. Japanese Soc. Sci. Fish.—Bulletin of the Japanese Society of Scientific Fisheries. Tokyo.

Bull. Pacific Sci. Fish. Inst.—Bulletins of the Pacific Scientific Fisheries Institute. Vladivostok.

Bull. Pacific Sci. Inst. Fish. and Oceanogr.—Bulletin of the Pacific Scientific Institute of Fisheries and Oceanography. Vladivostok.

Bull. Scripps Inst.—Bulletin. Scripps Institution for Biological Research. Berkeley.

Bull. So. Calif. Acad. Sci.—Bulletin of the Southern California Academy of Sciences. Los Angeles.

Bull. U. S. Fish Comm.—Bulletin of the United States Fish Commission. Washington.

Bur. Fish., Min. Agr. and For., Japanese Imp. Govt.—Bureau of Fisheries. Ministry of Agriculture and Forestry. Japanese Imperial Government. [Suisankyoku. Norinshō. Dai Nippon Teikoku Seifu.] Tokyo.

California Div. Fish and Game, Bur. Mar. Fish.—California Division of Fish and Game, Bureau of Marine Fisheries. San Francisco.

California Div. Fish and Game, Fish Bull.—California Division of Fish and Game. Fish Bulletin. Sacramento.

Cent. Fish. Expt. Sta. Rpt.—Central Fisheries Experiment Station Reports. [Suisan Shikenjō Chōsa Hōkoku.] Tokyo.

Com. Fish. Rev.—Commercial Fisheries Review. Fish and Wildlife Service. United States Department of the Interior. Washington.

Copeia—Copeia. New York.

Council Sci. and Indust. Res., Australia, Pamphlet—Council for Scientific and Industrial Research. Commonwealth of Australia. Pamphlet. Melbourne.

Dept. Fish., New South Wales—Department of Fisheries, New South Wales. Sydney.

Field Mus. Nat. Hist., Zool. Ser.—Field Museum of Natural History, Zoological Series. Chicago.

Fish. Div., FAO, UN.—Fisheries Division. The Food and Agriculture Organization of the United Nations. Washington.

Fish. Invest. (Suppl. Rpt.), Imp. Fish. Expt. Sta.—Fishery Investigation (Supplementary Report). Imperial Fisheries Experiment Station. Tokyo.

Fish. Res. Bd. Canada, Bull.—Fisheries Research Board of Canada, Bulletin. Vancouver.

Fish. Technol. Lect. Series—Fisheries Technology Lecture Series. [Suisan Seizō Kōgaku Kōza.] Tokyo.

Formosa Fish. Mag.—Formosa Fisheries Magazine. [Taiwan Suisan Zasshi.] Taihoku.

Formosa Govt.-Gen. Fish. Expt. Sta. Publ.—Formosa Government-General Fisheries Experiment Station. Publications. [Taiwan Sotokufu Suisan Shikenjō Shuppan.] Kiirun.

Ichth. Contrib. Internatl. Game Fish Assoc.—Ichthyological Contributions of the International Game Fish Association. New York.

Japanese Jour. Zool.—Japanese Journal of Zoology. Tokyo.

Jour. Acad. Nat. Sci. Phila.—Journal of the Academy of Natural Sciences of Philadelphia. Philadelphia.

Jour. Asiatic Soc. Bengal—Journal of the Asiatic Society of Bengal. Calcutta.

Jour. Biol. Chem.—Journal of Biological Chemistry. New York.

Jour. Coll. Agr., Imp. Univ. Tokyo—Journal of the College of Agriculture. Imperial University of Tokyo. Tokyo.

Jour. Coll. Sci., Imp. Univ. Tokyo—Journal of the College of Science. Imperial University of Tokyo. Tokyo.

Jour. Council Sci. and Indust. Res., Australia—Journal of the Council for Scientific and Industrial Research. Commonwealth of Australia. Melbourne.

Jour. Fac. Sci., Imp. Univ. Tokyo—Journal of the Faculty of Science, Imperial University of Tokyo. Tokyo.

Jour. Imp. Fish. Bur. Tokyo—Journal of the Imperial Fisheries Bureau. Tokyo.
Jour. Imp. Fish. Expt. Sta.—Journal of the Imperial Fisheries Experiment Station. Tokyo.
Jour. Mus. Godeffroy—Journal des Museum Godeffroy. Hamburg.
Jour. Pan-Pacific Res. Inst.—Journal of the Pan-Pacific Research Institution. Honolulu.

Mem. Bernice P. Bishop Mus.—Memoirs of the Bernice Panahi Bishop Museum. Honolulu.
Mem. California Acad. Sci.—Memoirs of the California Academy of Sciences. San Francisco.
Mem. Carnegie Mus.—Memoirs of the Carnegie Museum. Pittsburgh.
Mid-Pacific Mag.—Mid-Pacific Magazine. Honolulu.
Miyagi Pref. Fish. Expt. Sta.—Miyagi Prefectural Fisheries Experiment Station. [Miyagi-ken Suisan Shikenjō. Watanoha.

Nat. Geneesk. Arch. Neêrland's Indië—Natuur en Geneeskundig Archief voor Neêrland's-Indië. Batavia.
Nat. Tijdschr. Nederlandsch-Indië—Natuurkundig Tijdschrift voor Nederlandsch-Indië. Batavia.
Nederlandsch Tijdschr. Dierk.—Nederlandsch Tijdschrift voor de Dierkunde. Amsterdam.
New Zealand Jour. Sci. Technol.—New Zealand Journal of Science and Technology. Wellington.
New Zealand Mar. Dept. Fish. Bull.—New Zealand Marine Department Fisheries Bulletin. Wellington.
Nissan Fish. Res. Sta. Odawara—Nissan Fisheries Research Station. [Nissan Suisan Kenkyūjō.] Odawara.
Note Serv. Océanogr. Pêches Indochine—Notes. Service Océanographique des Pêches de l'Indochine. Station Maritime de Cauda. Saigon.

Occas. Pap. California Acad. Sci.—Occasional Papers of the California Academy of Sciences. San Francisco.
Ocean. Fish.—Oceanic Fisheries. [Kaiyō Gyogyō.] Tokyo.

Pacific Biol. Sta., Fish. Res. Bd. Canada, Circ.—Pacific Biological Stations, Fisheries Research Board of Canada. Vancouver.
Pacific Sci.—Pacific Science. Honolulu.
Palao Trop. Biol. Sta. Studies—Palao Tropical Biological Station Studies. Tokyo.
Philippine Jour. Sci.—Philippine Journal of Science. Manila.
Proc. Acad. Nat. Sci. Phila.—Proceedings of the Academy of Natural Sciences of Philadelphia. Philadelphia.
Proc. California Acad. Sci.—Proceedings of the California Academy of Sciences. San Francisco.
Proc. Sci. Fish. Assoc.—Proceedings of the Scientific Fisheries Association. Tokyo.
Proc. Sixth Pacific Sci. Cong.—Proceedings of the Sixth Pacific Science Congress. Berkeley and Los Angeles.
Proc. U. S. Natl. Mus.—Proceedings of the United States National Museum. Washington.
Proc. Zool. Acclim. Soc. Victoria—Proceedings of the Zoological and Acclimation Society of Victoria. Victoria.
Prog. Rpt. Chiba Pref. Fish. Expt. Sta.—Progress Reports of the Chiba Prefectural Fisheries Experiment Station. [Chiba-ken Suisan Shikenjō Jigyō Hōkoku.] Tateyama.
Prog. Rpt. Chiba Pref. Fish. Expt. Sta., Katsuura Br.—Progress Reports of the Chiba Prefectural Fisheries Experiment Station, Katsuura Branch. [Chiba-ken Suisan Shikenjō Katsuura Bunjō Jigyo Hōkoku.] Katsuura.
Prog. Rpt. Formosa Govt.-Gen. Fish. Expt. Sta.—Progress Reports of the Formosa Government-General Fisheries Experiment Station [Taiwan Sotokufu Suisan Shikenjō; Jigyō Hōkoku; Shiken Hōkoku; Suisan Shiken Hōkoku.] Kiirun.
Prog. Rpt. Hokkaidō Fish. Expt. Sta.—Progress Reports of the Hokkaidō Fisheries Experiment Station. [Hokkaidō Suisan Shikenjō Suisan Chōsa Hōkoku.] Yoichi.
Prog. Rpt. Kagoshima Pref. Fish. Expt. Sta.—Progress Reports of the Kagoshima Prefectural Fisheries Experiment Station. [Kagoshima-ken Suisan Shikenjō Jigyō Hōkoku.] Kagoshima.
Prog. Rpt. Kōchi Pref. Fish. Expt. Sta.—Progress Reports of the Kōchi Prefectural Fisheries Experiment Station. [Kōchi-ken Suisan Shikenjō Jigyō Hōkoku.] Susaki.
Prog. Rpt. Kumamoto Pref. Fish. Expt. Sta.—Progress Reports of the Kumamoto Prefectural Fisheries Experiment Station. [Kumamoto-ken Suisan Shikenjō Jigyō Hōkoku.] Kumamoto.
Prog. Rpt. Mie Pref. Fish. Expt. Sta.—Progress Reports of the Mie Prefectural Fisheries Experiment Station. [Mie-ken Suisan Shikenjō Jigyō Hōkoku.] Tsu.
Prog. Rpt. Nagasaki Pref. Fish. Expt. Sta.—Progress Reports of the Nagasaki Prefectural Fisheries Experiment Station. [Nagasaki-ken Suisan Shikenjō Jigyō Hōkoku.] Nagasaki.
Prog. Rpt. Ōita Pref. Fish. Expt. Sta.—Progress Reports of the Ōita Prefectural Fisheries Experiment Station. [Ōita-ken Suisan Shikenjō Gyōmu Hōkoku.] Ōita.
Prog. Rpt. Okinawa Pref. Fish. Expt. Sta.—Progress Reports of the Okinawa Prefectural Fisheries Experiment Station. [Okinawa-ken Suisan Shikenjō: Jigyō Hōkoku; Seiseki; Seiseki Gaiyō.] Naha.
Prog. Rpt. Pacific Coast Sta., Fish. Res. Bd. Canada—Reports of the Pacific Coast Stations, Fisheries Research Board of Canada. Vancouver.
Prog. Rpt. Shizuoka Pref. Fish. Expt. Sta.—Progress Reports of the Shizouka Prefectural Fisheries Experiment Station. [Shizuoka-ken Suisan Shikenjō Jigyō Hōkoku.] Shimizu.
Prog. Rpt. South Seas Govt.-Gen. Fish. Expt. Sta.—Progress Reports of the South Seas Government-General Fisheries Experiment Station. [Nanyō-chō Suisan Shikenjō Jigyō Hōkoku.] Palau.
Prog. Rpt. Taihoku Prov. Fish. Expt. Sta.—Progress Reports of the Taihoku Province Fisheries Experiment Station. [Taihoku-shū Suisan Shikenjō Gyōmu Hōkoku.] Taihoku.
Prog. Rpt. Takao Prov. Fish. Expt. Sta.—Progress Reports of the Takao Province Fisheries Experiment Station. [Takao-shū Suisan Shiken Chōsa Hōkoku.] Takao.
Publ. Field Mus. Nat. Hist.—Publications. Field Museum of Natural History. Chicago.

Rec. Canterbury Museum—Records of the Canterbury Museum. Christchurch.
Rec. Oceanogr. Works—Records of Oceanographic Works in Japan. Tokyo.
Rec. So. Australian Mus.—Records of the South Australian Museum. Adelaide.
Rpt. British Assoc. Adv. Sci.—Report of the British Association for the Advancement of Science. London.
Rpt. U. S. Fish Comm.—Report of the Commissioner. United States Commission of Fish and Fisheries. Washington.

SCAP Nat. Resources Sec. Rpt.—Supreme Commander for the Allied Powers. General Headquarters. Natural Resources Section. Reports. Tokyo.
Sci. Sea—Science of the Sea. [Kaiyō no Kagaku.]
Sea and Sky—Sea and Sky. [Umi to Sora.] Kobe.
Semi-Ann. Rpt. Oceanogr. Invest.—Semi-Annual Report of Oceanographical Investigations. Tokyo.
Smithsn. Misc. Collect.—Smithsonian Miscellaneous Collections. Washington.
Soc. Prom. Ocean. Fish.—Society for the Promotion of Oceanic Fisheries. [Kaiyō Gyogyō Kyokai.] Tokyo.
South Sea Fish.—South Sea Fisheries. [Nanyō Suisan.] Tokyo.
South Sea Fish. News—South Sea Fisheries News. [Nanyō Suisan Jōhō.] Palau.
South Sea Sci.—South Sea Science. [Kagaku Nanyō.] Palau.
Stanford Ichth. Bull.—Stanford Ichthyological Bulletin. Stanford.
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INDEX BY SUBJECTS

Age
Aikawa, 1937.
Aikawa and Kato, 1938.
Ban, 1941.
Brock, 1943.
Higashi, 1941b.
Ikebe, 1939, 1940a, 1940b, 1940c, 1941a, 1941b.
Kanamura and Yazaki, 1940a, 1940b.
Kimura, 1935, 1941, 1942a.
Okamoto, 1940.
Schaefer, 1948b.
Tauchi, 1940a, 1940b, 1940c.
Uno, 1936b.
Yabe and Mori, 1948.
Albacore. See *Thunnus germo.*
Allison's tuna. See *Neothunnus allisoni.*
Allothunnus fallai
Anatomy
Serventy, 1948.
Classification
Fraser-Brunner, 1950.
Serventy, 1948.
Compared with Katsuwonidae
Serventy, 1948.
Description
Fraser-Brunner, 1950.
Serventy, 1948.
Distribution
Fraser-Brunner, 1950.
Serventy, 1948.
Figured
Fraser-Brunner, 1950.
Serventy, 1948.
Keys
Fraser-Brunner, 1950.
Measurement data
Serventy, 1948.
Synonymy
Fraser-Brunner, 1950.
Anatomy
Air bladder
Fish, 1948.
Kishinouye, 1922a.
And evolution
Kishinouye, 1919a.
Brain
Matsui, 1942a.
Migita and Arakawa, 1948.
Digestive system
Suyehiro, 1936, 1938, 1941, 1942.
External and internal
Berg, 1947.
Eckles, 1949b.
Godsil and Byers, 1944.
Imamura, 1949.
Anatomy—Continued
External and internal—Continued
Kishinouye, 1915a, 1915b, 1917a, 1918, 1921, 1923.
Nakamura, 1949.
Roedel, 1948b.
Schaefer and Marr, 1948b.
Serventy, 1942b, 1948.
Takahashi, 1924.
Figured
Godsil and Byers, 1944.
Higashi, 1941a, 1941c.
Kishinouye, 1915b, 1919a, 1923.
Matsui, 1942b.
Migita and Arakawa, 1948.
Nakamura, 1938.
Serventy, 1941, 1942b, 1948.
Suyehiro, 1942.
Reproductive system
Bennett, 1840.
Matsui, 1942b.
Nakamura, 1938.
Nakamura Res. Staff, 1949.
Okinawa Pref. Fish. Expt. Sta., 1931.
Astronomical phenomena correlated with fishing
Kawana, 1934.
Takao Prov. Fish. Expt. Sta., 1927.
Auxis
Anatomy
Kishinouye, 1915b, 1919a.
As food of tunas
Asano, 1939.
Chemical analysis
Okuda, 1918.
Common names
Tominaga, 1943.
Description
Tominaga, 1943.
Distribution
Schaefer, 1948c.
Tominaga, 1943.
Food
Tominaga, 1943.
Habits
Tominaga, 1943.
Hormones
Migita and Arakawa, 1948.
Reproduction
Schaefer, 1948c.
Young
Kishinouye, 1926.
Schaefer, 1948c.
Auxis hira
Anatomy
Kishinouye, 1915a, 1923.

Auxis hira—Continued
Classification
Kishinouye, 1915a, 1923.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Common names
Fujita and Wakiya, 1915.
Kishinouye, 1915a, 1923.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Shapiro, 1948b.
Description
Imamura, 1949.
Jordan and Hubbs, 1925.
Kishinouye, 1915a, 1923.
Okada and Matsubara, 1938.
Soldatov and Lindberg, 1930.
Distribution
Fujita and Wakiya, 1915.
Imamura, 1949.
Jordan and Hubbs, 1925.
Kishinouye, 1915a, 1923.
Okada and Matsubara, 1938.
Shapiro, 1948b.
Soldatov and Lindberg, 1930.
Tanaka, 1931.
Taranetz, 1937.
Figured
Kishinouye, 1915a, 1923.
Food
Kishinouye, 1923.
Habits
Imamura, 1949.
Kishinouye, 1923.
Keys
Kishinouye, 1915a, 1923.
Okada and Matsubara, 1938.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Synonymy
Kishinouye, 1923.
Nakamura, 1939b.
Soldatov and Lindberg, 1930.
Tanaka, 1931.

Auxis maru
Anatomy
Kishinouye, 1915a, 1923.
Classification
Kishinouye, 1915a, 1923.
Nakamura, 1939b.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Common names
Fujita and Wakiya, 1915.
Kishinouye, 1915a, 1923.
Nakamura, 1939b.

Auxis maru—Continued
Description
Imamura, 1949.
Kishinouye, 1915a, 1923.
Soldatov and Lindberg, 1930.
Distribution
Fujita and Wakiya, 1915.
Imamura, 1949.
Kishinouye, 1915a, 1923.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Figured
Kishinouye, 1915a, 1923.
Food
Kishinouye, 1923.
Habits
Imamura, 1949.
Kishinouye, 1923.
Keys
Kishinouye, 1915a, 1923.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Reproduction
Kishinouye, 1915a.
Synonymy
Kishinouye, 1923.
Nakamura, 1939b.
Soldatov and Lindberg, 1930.
Young as food of tunas
Kishinouye, 1917b, 1923, 1924.

Auxis ramsayi
Distribution
McCulloch, 1922.
Keys
McCulloch, 1922.
Synonymy
McCulloch, 1922.

Auxis rochei
Description
Günther, 1860.
Distribution
Chu, 1931.
Günther, 1860.
Synonymy
Chu, 1931.
Günther, 1860.

Auxis tapeinosoma
Classification
Okada and Matsubara, 1938.
Wade, 1949.
Common names
Jordan and Hubbs, 1925.
Jordan and Snyder, 1901.
Okada and Matsubara, 1938.
Shapiro, 1948b.
Compared with *Auxis thynnoides*
Bleeker, 1855.
Description
Bleeker, 1854.
Günther, 1860.

Auxis tapeinosoma—Continued
Description—Continued
Jordan and Hubbs, 1925.
Okada and Matsubara, 1938.
Wade, 1949.
Distribution
Bleeker, 1854, 1857.
Günther, 1860.
Jordan and Hubbs, 1925.
Jordan and Snyder, 1901.
Okada and Matsubara, 1938.
Reeves, 1928.
Shapiro, 1948b
Wade, 1949.
Figured
Wade, 1949.
Keys
Okada and Matsubara, 1938.
Wade, 1949.
Measurement data
Wade, 1949.
Meristic characters
Wade, 1949.
Synonymy
Günther, 1860.
Jordan and Hubbs, 1925.
Wade, 1949.
Young
Wade, 1949.
Auxis taso
Compared with *Auxis thynnoides*
Bleeker, 1855.
Description
Cuvier and Valenciennes, 1831.
Distribution
Bleeker, 1845, 1850, 1878.
Auxis thazard
Anatomy
Schaefer and Marr, 1948b.
As food of tunas
Marukawa, 1939.
Classification
Fraser-Brunner, 1950.
Common names
Barnhart, 1936.
FAO, 1949.
Fish, 1948.
Herre and Umali, 1948.
Jordan and Evermann, 1896.
Jordan and Metz, 1913.
Jordan, Tanaka, and Snyder, 1913.
Serventy, 1941.
Tinker, 1944.
Ulrey and Greeley, 1928.
Walford, 1937.
Description
Barnhart, 1936.
Cuvier and Valenciennes, 1831.
Fowler, 1928, 1938.
Fraser-Brunner, 1950.
Auxis thazard—Continued
Description—Continued
Jordan and Evermann, 1905.
Meek and Hildebrand, 1923.
Schaefer and Marr, 1948b.
Serventy, 1941.
Tinker, 1944.
Wade, 1949.
Walford, 1937.
Distribution
Barnhart, 1936.
Domantay, 1940.
FAO, 1949.
Fish, 1948.
Fowler, 1928, 1938, 1944, 1949.
Fraser-Brunner, 1950.
Graham, 1938.
Herre, 1940.
Jenkins, 1903.
Jordan and Evermann, 1896, 1905.
Jordan and Jordan, 1922.
Jordan and Metz, 1913.
Jordan and Seale, 1906.
Jordan and Snyder, 1900.
Jordan, Tanaka, and Snyder, 1913.
Lord, 1927.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Mori, 1928.
Reeves, 1928.
Schaefer and Marr, 1948b.
Serventy, 1941.
Soldatov, 1929.
Stead, 1908.
Thompson and Higgins, 1919.
Tinker, 1944.
Ulrey, 1929.
Ulrey and Greeley, 1928.
Wade, 1949.
Walford, 1937.
Figured
Barnhart, 1936.
Domantay, 1940.
Fraser-Brunner, 1950.
Jordan and Evermann, 1905.
Jordan, Tanaka, and Snyder, 1913.
McCulloch, 1922.
Schaefer and Marr, 1948b.
Serventy, 1941.
Tinker, 1944.
Wade, 1949.
Walford, 1937.
Keys
Brock, 1949.
Fraser-Brunner, 1950.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Serventy, 1941.
Wade, 1949.
Walford, 1937.

Auxis thazard—Continued
Measurement data
Wade, 1949.
Meristic characters
Schaefer and Marr, 1948b.
Wade, 1949.
Synonymy
FAO, 1949.
Fowler, 1928, 1938, 1944, 1949.
Fraser-Brunner, 1950.
Jenkins, 1903.
Jordan and Evermann, 1896, 1905.
Jordan, Tanaka, and Snyder, 1913.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Ulrey and Greeley, 1928.
Wade, 1949.
Young
Schaefer and Marr, 1948b.
Wade, 1949.
Young as food of tunas
Marukawa, 1939.
Auxis thynnoides
Compared with *Auxis tapeinosoma*
Bleeker, 1855.
Compared with *Auxis taso*
Bleeker, 1855.
Compared with *Auxis vulgaris*
Bleeker, 1855.
Description
Bleeker, 1855.
Distribution
Bleeker, 1855, 1863, 1865a.
Auxis vulgaris
Compared with *Auxis thynnoides*
Bleeker, 1855.

Bibliography
Corwin, 1930.
Kishinouye, 1923.
Nakamura, 1949.
Shapiro, 1948a, 1948b.
Big-eyed tuna. See *Parathunnus* spp.
Black tuna. See *Thunnus orientalis.*
Bluefin tuna. See *Thunnus thynnus.*
Body condition
Aikawa, 1937.
Aikawa and Kato, 1938.
Ikebe, 1939.
Ikebe and Matsumoto, 1937.
Kanamura and Yazaki, 1940a, 1940b.
Onodera, 1941.
Soc. Prom. Ocean. Fish., 1936.
South Seas Govt.–Gen. Fish. Expt. Sta., 1941d.
Suyehiro, 1936, 1938.
Body temperature
Anonymous, 1938.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Body temperature—Continued
Nakamura, 1941.
Ōita Pref. Fish. Expt. Sta., 1927a, 1930.
Seagel, 1949.
Uda, 1941.
Watanabe, N., 1941.
Bonito. See *Katsuwonus pelamis.*

Catch per unit of effort
Formosa Govt.–Gen. Fish. Expt. Sta., 1933a.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Imaizumi, 1937.
Japanese Bur. Fish., 1939, 1940.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Nakamura, 1949.
Okuma, Imaizumi, and Maki, 1935.
Serventy, 1947.
Whitehead, 1931.
Characters, meristic. See Morphometrics.
Chemical analysis
Dill, 1921.
Higashi and Hirai, 1948.
Kodama, Iizuka, and Harada, 1934.
Miyama and Osakabe, 1938, 1940.
Miyama, Saruya, and Hasegawa, 1939.
Miyauchi, 1915.
Okuda, 1918.
Shimizu, 1947.
Soc. Prom. Ocean. Fish., 1936.
Tomiyama, 1933.
Classification
Berg, 1947.
Fraser-Brunner, 1949, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Jordan, 1923.
Kishinouye, 1915a, 1917a, 1923.
Lacépède, 1829.
Lütken, 1880.
Nakamura, 1939a, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Phillipps, 1927b.
Roedel, 1948b.
Roughly, 1916.
Schaefer, 1948a.
Serventy, 1948.
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Takahashi, 1924, 1926.
Taranetz, 1937.
Wade, 1949.
Walford, 1931.
Whitehead, 1931.
Whitley, 1937.
Color, water. See Water color, also Oceanographic conditions.
Condition, body. See Body condition.
Contents, stomach. See Food.

Currents. See also Oceanographic conditions.
Correlated with fishing
Formosa Govt.-Gen. Fish. Expt. Sta., 1930, 1931, 1932, 1933b, 1934.
Ikebe, 1940d.
Inanami, 1940b, 1940c, 1941.
Kagoshima Pref. Fish. Expt. Sta., 1927b, 1928a.
South Seas Govt.-Gen. Fish. Expt. Sta., 1942, 1943b.

Distribution
Abe, 1939.
Anonymous, 1938, 1941.
Barnhart, 1936.
Bleeker, 1844, 1845, 1850, 1852, 1854, 1855, 1856, 1857, 1860a, 1860b, 1861a, 1861b, 1862, 1863, 1865a, 1865b, 1878, 1879.
Brock, 1938, 1939.
Cantor, 1850.
Chabanaud, 1926.
Chapman, 1946.
Chevey, 1932a, 1932b.
Chu, 1931.
Clemens and Wilby, 1946.
Cooper, 1863.
Cowan, 1938.
Cuvier and Valenciennes, 1831.
Delsman and Hardenburg, 1934
Domantay, 1940.
Eckles, 1949a, 1949b.
Eigenmann, 1892.
Eigenmann and Eigenmann, 1890, 1891.
Evermann and Seale, 1907.
FAO, 1949.
Fish, 1948.
Fowler, 1904a, 1923a, 1923b, 1927, 1928, 1929, 1931, 1934, 1938, 1944, 1949.
Fowler and Ball, 1925.
Fraser-Brunner, 1949, 1950
Fujita and Wakiya, 1915.
Gilbert and Starks, 1904.
Godsil and Greenhood, 1948.
Graham, 1938.
Griffin, 1927.
Günther, 1860, 1876.
Hasegawa, 1937.
Herre, 1932, 1933, 1935, 1936, 1940.
Hildebrand, 1946.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Holder, 1912.
Hubbs, 1916, 1928
Imaizumi, 1937.
Imamura, 1949.
Japanese Bur. Fisb., 1934, 1939, 1940.
Jenkins, 1903.
Jordan, 1885.
Jordan and Evermann, 1896, 1905, 1926a, 1926b.
Jordan and Gilbert, 1881a, 1882.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Distribution—Continued
Jordan and Metz, 1913.
Jordan and Seale, 1906.
Jordan and Snyder, 1900, 1901.
Jordan and Starks, 1907.
Jordan, Tanaka, and Snyder, 1913.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Kimura, 1941, 1942b.
Kishinouye, 1915a, 1919c, 1922c, 1923.
Kōchi Pref. Fisb. Expt. Sta., 1923b, 1924.
Kumata et al., 1941.
Lesson, 1830.
Lord, 1927.
Macleay, 1881.
Martin, 1938.
Matsubara, 1943.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Metz, 1912.
Mori, 1928.
Nakamura, 1938, 1939b, 1943, 1949.
Nichols and Murphy, 1922, 1944.
Okada and Matsubara, 1938.
Okinawa Pref. Fish. Expt. Sta., 1943.
Okuma, Imaizumi, and Maki, 1935.
Phillipps, 1927a, 1927b.
Phillipps and Hodgkinson, 1922.
Powell, 1937.
Reeves, 1928.
Richardson, 1846.
Roedel, 1948a, 1948b.
Roughly, 1916.
Samson, 1940.
Schaefer, 1948c.
Schmidt, 1930.
Schmitt and Schultz, 1940.
Schultz, 1949.
Schultz and DeLacy, 1936.
Seale, 1940.
Serventy, 1941, 1942a, 1942b, 1947, 1948.
Shapiro, 1948a, 1948b.
Smith and Schaefer, 1949.
Snyder, 1904.
Soldatov, 1929.
Soldatov and Lindberg, 1930.
South Seas Govt.-Gen. Fish. Expt. Sta., 1937a, 1937b, 1941a.
Starks, 1918.
Starks and Morris, 1907.
Stead, 1906, 1908.
Takao Prov. Fish. Expt. Sta., 1927.
Tanaka, 1912, 1931.
Taranetz, 1937.
Thompson and Higgins, 1919.
Tinker, 1944.
Tirant, 1929.
Tominaga, 1943.
Tubb, 1948.
Ulrey, 1929.

Distribution—Continued
Ulrey and Greeley, 1928.
Wade, 1949.
Waite, 1907, 1921, 1928.
Walford, 1931, 1937.
Weber, 1913.
Whitehead, 1929, 1931.
Whitley, 1928, 1937, 1947.
Distribution correlated with water temperature
Takayama and Ando, 1934.
Takayama, Ideda, and Ando, 1934.
Uda, 1935a, 1935b, 1936, 1940b.

Eggs
DeJong, 1940.
Delsman, 1931.
Delsman and Hardenburg, 1934.
Hatai et al., 1941.
Marr, 1948.
Nakamura, 1938, 1949.
Nakamura Res. Staff, 1949.
Watanabe, H., 1939.
Yabe and Mori, 1948.
Enemies
Bennett, 1840.
Imamura, 1949.
Kishinouye, 1923.
Tinker, 1944.
Walford, 1937.

Euthynnus
Common names
Fish, 1948.
Distribution
Fish, 1948.

Euthynnus alleterata. See *Euthynnus alletteratus.*

Euthynnus alleteratus. See *Euthynnus alletteratus.*

Euthynnus alletteratus
Classification
Hildebrand, 1946.
Okada and Matsubara, 1938.
Common names
Delsman and Hardenburg, 1934.
FAO, 1949.
Jordan and Evermann, 1905.
Jordan and Jordan, 1922.
Jordan and Snyder, 1901.
Jordan, Tanaka, and Snyder, 1913.
Okada and Matsubara, 1938.
Serventy, 1941.
Tinker, 1944.
Whitley, 1947.
Compared with *Euthynnus lineatus*
Schmitt and Schultz, 1940.
Compared with Mediterranean *Thynnus thunnina*
Temminck and Schlegel, 1850.
Compared with *Thynnus pelamys*
Cantor, 1850.
Compared with *Wanderer wallisi*
Whitley, 1937.

Euthynnus alletteratus—Continued
Description
Boeseman, 1947.
Cantor, 1850.
Delsman and Hardenburg, 1934.
Fowler, 1904b, 1928.
Günther, 1860, 1876.
Hildebrand, 1946.
Jordan and Evermann, 1905.
Macleay, 1881.
Meek and Hildebrand, 1923.
Okada and Matsubara, 1938.
Serventy, 1941.
Tinker, 1944.
Distribution
Bleeker, 1852, 1860a, 1860b, 1861a, 1861b, 1862, 1865a, 1865b.
Cantor, 1850.
Chabanaud, 1926.
Chapman, 1946.
Delsman and Hardenburg, 1934.
FAO, 1949.
Fowler, 1928, 1931, 1938, 1944.
Fowler and Ball, 1925.
Günther, 1860, 1876.
Herre, 1932, 1940.
Hildebrand, 1946.
Jenkins, 1903.
Jordan and Evermann, 1905.
Jordan and Jordan, 1922.
Jordan and Seale, 1906.
Jordan and Snyder, 1901.
Jordan, Tanaka, and Snyder, 1913.
Macleay, 1881.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Okada and Matsubara, 1938.
Richardson, 1846.
Schmidt, 1930.
Schmitt and Schultz, 1940.
Serventy, 1941.
Stead, 1908.
Tanaka, 1931.
Tinker, 1944.
Tirant, 1929.
Weber, 1913.
Whitley, 1947.
Eggs
DeJong, 1940.
Delsman, 1931.
Delsman and Hardenburg, 1934.
Figured
Delsman and Hardenburg, 1934.
Fowler, 1928.
Günther, 1876.
Jordan and Evermann, 1905.
Jordan, Tanaka, and Snyder, 1913.
Kitahara, 1897.
Serventy, 1941.
Temminck and Schlegel, 1850.
Tinker, 1944.

Euthynnus alletteratus—Continued
Food
Hildebrand, 1946.
Keys
Delsman and Hardenburg, 1934.
Hildebrand, 1946.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Okada and Matsubara, 1938.
Serventy, 1941.
Parasites
Manter, 1940.
Van Cleave, 1940.
Reproduction
Delsman and Hardenburg, 1934.
Synonymy
Boeseman, 1947.
Chevey, 1934.
FAO, 1949.
Fowler, 1904b, 1928.
Günther, 1860. 1876.
Hildebrand, 1946.
Jenkins, 1903.
Jordan and Evermann, 1905.
Jordan, Tanaka, and Snyder, 1913.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Richardson, 1846.
Tanaka, 1931.
Weber, 1913.
Young
Delsman, 1931.
Delsman and Hardenburg, 1934.
Günther, 1889.
Euthynnus allitteratus. See *Euthynnus alletteratus*.
Euthynnus lineatus
Anatomy
Kishinouye, 1923.
Schaefer and Marr, 1948b.
Classification
Fraser-Brunner, 1949.
Kishinouye, 1923.
Common names
Kishinouye, 1923.
Walford, 1937.
Compared with *Euthynnus alletteratus*
Schmitt and Schultz, 1940.
Description
Fowler, 1938.
Kishinouye, 1919c, 1923.
Schaefer and Marr, 1948b.
Seale, 1940.
Walford, 1937.
Distribution
Fowler, 1938, 1944.
Fraser-Brunner, 1949.
Kishinouye, 1919c, 1923.
Roedel, 1948a.
Schaefer, 1948c.
Schaefer and Marr, 1948b.
Euthynnus lineatus—Continued
Description—Continued
Schmitt and Schultz, 1940.
Seale, 1940.
Walford, 1937.
Figured
Fowler, 1944.
Fraser-Brunner, 1949.
Kishinouye, 1923.
Schaefer and Marr, 1948b.
Walford, 1937.
Food
Kishinouye, 1923.
Walford, 1937.
Habits
Kishinouye, 1923.
Keys
Fraser-Brunner, 1949.
Kishinouye, 1923.
Walford, 1937.
Meristic characters
Schaefer and Marr, 1948b.
Reproduction
Schaefer, 1948c.
Walford, 1937.
Synonymy
Fowler, 1938, 1944.
Fraser-Brunner, 1949.
Kishinouye, 1923.
Young
Schaefer, 1948c.
Schaefer and Marr, 1948b.
Euthynnus macroptera
Distribution
Tubb, 1948.
Euthynnus pelamis. See *Katsuwonus pelamis*.
Euthynnus pelamys. See *Katsuwonus pelamis*.
Euthynnus vagans. See *Katsuwonus pelamis*.
Euthynnus wallisi
Distribution
Fowler, 1949.
Synonymy
Fowler, 1949.
Euthynnus yaito
Anatomy
Kishinouye, 1915a, 1915b, 1919a, 1923.
Chemical analysis
Miyauchi, 1915.
Classification
Fraser-Brunner, 1949.
Kishinouye, 1915a, 1923.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Common names
Chevey, 1932a.
Fujita and Wakiya, 1915.
Herre and Umali, 1948.
Kishinouye, 1915a, 1923.
Nakamura, 1939b.
Okada and Matsubara, 1938.

Euthynnus yaito—Continued
Common names—Continued
Shapiro, 1948b.
Tominaga, 1943.
Compared with *Wanderer wallisi*
Whitley, 1937.
Description
Chevey, 1932a.
Kishinouye, 1915a, 1923.
Okada and Matsubara, 1938.
Tominaga, 1943.
Distribution
Chevey, 1932a, 1932b.
Domantay, 1940.
Eckles, 1949a.
Fraser-Brunner, 1949.
Fujita and Wakiya, 1915.
Godsil and Greenhood, 1948.
Herre, 1933, 1940.
Jordan and Evermann, 1926a.
Jordan and Hubbs, 1925.
Kishinouye, 1915a, 1922c, 1923.
Okada and Matsubara, 1938.
Schaefer, 1948c.
Shapiro, 1948b.
Smith and Schaefer, 1949.
Tominaga, 1943.
Figured
Chevey, 1932a.
Domantay, 1940.
Fraser-Brunner, 1949.
Kishinouye, 1915a, 1923.
Smith and Schaefer, 1949.
Food
Herald, 1949.
Kishinouye, 1923.
Tominaga, 1943.
Welsh, 1949.
Habits
Kishinouye, 1923.
Tominaga, 1943.
Keys
Brock, 1949.
Fraser-Brunner, 1949.
Kishinouye, 1915a, 1923.
Okada and Matsubara, 1938.
Measurement data
Bonham, 1946.
Parasites
Kishinouye, 1923.
Reproduction
Kishinouye, 1923.
Schaefer, 1948c.
Synonymy
Chevey, 1932a, 1934.
Fraser-Brunner, 1949.
Jordan and Hubbs, 1925.
Kishinouye, 1923.
Nakamura, 1939b.
Euthynnus yaito—Continued
Young
Kishinouye, 1919b, 1923, 1924.
Schaefer, 1948c.
Euthynnus alletteratus. See *Euthynnus alletteratus.*
Evolution
Based on internal anatomy
Kishinouye, 1919a.
Exploitation rates
Tauchi, 1940a, 1940b, 1940c.

Fishing conditions
Correlated with area
Hart and Hollister, 1947.
Hart et al., 1948.
Correlated with astronomical phenomena. See Astronomical phenomena.
Correlated with oceanography. See Oceanographic conditions.
Correlated with season
Hart et al., 1948.
Inanami, 1942b.
Whitehead, 1929.
Fishing grounds
Location correlated with oceanography. See Oceanographic conditions.
Food
Anonymous, 1938.
Asano, 1939.
Ban, 1941.
Bennett, 1840.
Chapman, 1946.
Clemens and Wilby, 1946.
Delsman and Hardenburg, 1934.
Eckles, 1949b.
Fitch, 1950.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Hart and Hollister, 1947.
Hart et al., 1948.
Hatai et al., 1941.
Herald, 1949.
Hildebrand, 1946.
Imamura, 1949.
Japanese Bur. Fish., 1934, 1939, 1940.
Jordan and Gilbert, 1881b, 1882.
Kanamura and Yazaki, 1940a, 1940b.
Kishinouye, 1895, 1915a, 1917b, 1923.
Kuronuma, 1940.
Marukawa, 1939.
Miyama, Saruya, and Hasegawa, 1939.
Nakamura, 1936, 1943, 1949.
Nakamura Res. Staff, 1949.
Okuma, Imaizumi, and Maki, 1935.
Seagel, 1949.
Serventy, 1942a.
Shapiro, 1948a.
Starks, 1918.
Starks and Morris, 1907.
Suyehiro, 1936, 1938, 1942.
Taihoku Prov. Fish. Expt. Sta., 1928, 1929.

Food—Continued
Tinker, 1944.
Tominaga, 1943.
Walford, 1937.
Watanabe, H., 1939.
Welsh, 1949.
Whitley, 1937.
Yabe and Mori, 1948.

Germo alalunga. See *Thunnus germo.*
Germo alalunga. See *Thunnus germo.*
Germo albacores. See *Neothunnus itosibi.*
Germo argentivittatus. See *Neothunnus argentivittatus.*
Germo germo. See *Thunnus germo.*
Germo germon. See *Thunnus germo.*
Germo macropterus. See *Neothunnus macropterus.*
Germo sibi. See *Parathunnus sibi.*
Gravity, specific. See Specific gravity, also Oceanographic conditions.
Growth
Aikawa and Kato, 1938.
Brock, 1943.
Kimura, 1932, 1935.
Kishinouye, 1923.
Schaefer, 1948a, 1948b.
Gymnosarda affinis. See *Katsuwonus pelamis.*
Gymnosarda alletterata. See *Euthynnus alletteratus.*
Gymnosarda pelamis. See *Katsuwonus pelamis.*

Habits
Brock, 1949.
Imamura, 1949.
Jordan and Gilbert, 1882.
Kida, 1936.
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Roughly, 1916.
Schaefer, 1948b.
Serventy, 1942a.
Shapiro, 1948a.
Tinker, 1944.
Tominaga, 1943.
Uchida, 1923.
Uda, 1935b, 1940a.
Uda and Tsukushi, 1934.
Hermaphroditism
Nakamura, 1935.
Hormones
Migita and Arakawa, 1948.
Oya and Takahashi, 1936.
Toyama et al., 1941.

Juveniles. See Young.

Katsuwonidae
Anatomy
Kishinouye, 1917a, 1919a
Classification
Kishinouye, 1917a.
Compared with *Allothunnus fallai*
Serventy, 1948.
Katsuwonidae—Continued
Keys
Jordan and Hubbs, 1925.
Katsuwonus pelamis
Age
Aikawa, 1937.
Aikawa and Kato, 1938.
Higashi, 1941b.
Kimura, 1941.
Okamoto, 1940.
Yabe and Mori, 1948.
Anatomy
Eckles, 1949b.
Godsil and Byers, 1944.
Higashi, 1941a.
Imamura, 1949.
Kishinouye, 1915a, 1915b, 1918, 1919a, 1923.
Matsui, 1942a, 1942b.
Suyehiro, 1936, 1938, 1941, 1942.
Body condition
Aikawa, 1937.
Aikawa and Kato, 1938.
Ikebe and Matsumoto, 1937.
Onodera, 1941.
South Seas Govt.-Gen. Fish. Expt. Sta., 1941d.
Suyehiro, 1936, 1938.
Body temperature
Uda, 1941.
Watanabe, N., 1941.
Catch per unit of effort
Kanamura and Yazaki, 1940a, 1940b.
Chemical analysis
Higashi and Hirai, 1948.
Kodama, Iizuka, and Harada, 1934.
Miyama and Osakabe, 1938, 1940.
Miyauchi, 1915.
Okuda, 1918.
Classification
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Kishinouye, 1915a, 1923.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Phillipps, 1927b.
Roedel, 1948b.
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931.
Common names
Barnhart, 1936.
Craig, 1929.
Delsman and Hardenburg, 1934.
FAO, 1949.
Fish, 1948.
Fujita and Wakiya, 1915.
Herre and Umali, 1948.
Jordan and Evermann, 1896, 1905.
Jordan and Hubbs, 1925.

Katsuwonus pelamis—Continued
Common names—Continued
Jordan and Jordan, 1922.
Jordan and Snyder, 1901.
Jordan, Tanaka, and Snyder, 1913.
Kishinouye, 1915a, 1923.
Kumata et al., 1941.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Phillipps, 1927b.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a, 1948b.
Smith, 1947.
Starks and Morris, 1907.
Tanaka, 1912.
Tinker, 1944.
Tominaga, 1943.
Ulrey and Greeley, 1928.
Walford, 1931, 1937.
Whitley, 1947.
Compared with *Thynnus affinis*
Cantor, 1850.
Description
Barnhart, 1936.
Bennett, 1840.
Bleeker, 1856.
Boeseman, 1947.
Clemens and Wilby, 1946.
Cuvier and Valenciennes, 1934.
Delsman and Hardenburg, 1934.
Eigenmann and Eigenmann, 1890.
Fowler, 1928, 1938.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Günther, 1860, 1876.
Hildebrand, 1946.
Imamura, 1949.
Jordan and Evermann, 1905.
Kishinouye, 1915a, 1922b, 1923.
Lesson, 1830.
Macleay, 1881.
Meek and Hildebrand, 1923.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Roedel, 1948b.
Seale, 1940.
Serventy, 1941.
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Stead, 1906.
Tanaka, 1912.
Temminck and Schlegel, 1850.
Tinker, 1944.
Tominaga, 1943.
Walford, 1931, 1937.
Distribution
Abe, 1939.
Anonymous, 1941.
Barnhart, 1936.

Katsuwonus pelamis—Continued
Distribution—Continued
Bleeker, 1856, 1860a, 1862, 1865a.
Chapman, 1946.
Clemens and Wilby, 1946.
Cuvier and Valenciennes, 1831.
Delsman and Hardenburg, 1934.
Domantay, 1940.
Eckles, 1949a.
Eigenmann, 1892.
Eigenmann and Eigenmann, 1890, 1891.
Evermann and Seale, 1907.
FAO, 1949.
Fish, 1948.
Fowler, 1928, 1931, 1934, 1938, 1944, 1949.
Fraser-Brunner, 1950.
Fujita and Wakiya, 1915.
Godsil and Greenhood, 1948.
Günther, 1860, 1876.
Herre, 1932, 1933, 1935, 1936, 1940.
Hildebrand, 1946.
Imamura, 1949.
Jenkins, 1903.
Jordan and Evermann, 1896, 1905.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Jordan and Seale, 1906.
Jordan and Snyder, 1901.
Jordan and Starks, 1907.
Jordan, Tanaka, and Snyder, 1913.
Kanamura and Yazaki, 1940a, 1940b.
Kimura, 1941, 1942b.
Kishinouye, 1915a, 1923.
Kumata et al., 1941.
Lesson, 1830.
Macleay, 1881.
Martin, 1938.
Matsubara, 1943.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Nakamura, 1939b.
Nichols and Murphy, 1944.
Okada and Matsubara, 1938.
Okinawa Pref. Fish. Expt. Sta., 1943.
Phillipps, 1927a, 1927b.
Phillipps and Hodgkinson, 1922.
Reeves, 1928.
Richardson, 1846.
Roedel, 1948b.
Roughly, 1916.
Schaefer, 1948c.
Seale, 1940.
Serventy, 1941, 1947.
Shapiro, 1948a, 1948b.
Smith and Schaefer, 1949.
Soldatov and Lindberg, 1930.
South Seas Govt.-Gen. Fish. Expt. Sta., 1937a.
Starks and Morris, 1907.
Stead, 1906, 1908.
Tanaka, 1912, 1931.

Katsuwonus pelamis—Continued
Distribution—Continued
Taranetz, 1937.
Tinker, 1944.
Tominaga, 1943.
Ulrey, 1929.
Ulrey and Greeley, 1928.
Waite, 1907.
Walford, 1931, 1937.
Whitehead, 1929.
Whitley, 1947.
Distribution correlated with water temperature
Takayama, Ikeda, and Ando, 1934.
Uda, 1935b, 1936, 1940b.
Eggs
Hatai et al., 1941.
Marr, 1948.
Nakamura Res. Staff, 1949.
Yabe and Mori, 1948.
Enemies
Imamura, 1949.
Tinker, 1944.
Figured
Barnhart, 1936.
Clemens and Wilby, 1946.
Cuvier and Valenciennes, 1831.
Domantay, 1940.
Eckles, 1949a.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Jordan and Evermann, 1905.
Kishinouye, 1915a, 1923.
Kitahara, 1897.
Kumata et al., 1941.
Lesson, 1830.
McCulloch, 1922.
Nakamura, 1939b.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a.
Smith and Schaefer, 1949.
Tanaka, 1912.
Temminck and Schlegel, 1850.
Tinker, 1944.
Walford, 1931, 1937.
Fishing conditions correlated with oceanography
Aikawa, 1933.
Chiba Pref. Fish. Expt. Sta., Katsuura Br., 1936, 1937, 1938, 1941.
Formosa Govt.-Gen. Fish. Expt. Sta., 1930, 1931, 1932, 1933b, 1934.
Imamura, 1949.
Inanami, 1941, 1942d.
Kagoshima Pref. Fish. Expt. Sta., 1925, 1926a, 1926b, 1927b, 1928a, 1929a, 1930a, 1931a, 1932a, 1933a, 1935, 1936a, 1937.
Kanamura and Yazaki, 1940b.
Kawamura, 1939.
Kimura, 1941, 1949.
Kōchi Pref. Fish. Expt. Sta., 1923a.
Katsuwonus pelamis—Continued
Fishing conditions correlated with oceanography—Con.
Kumamoto Pref. Fish. Expt. Sta., 1946.
Mie Pref. Fish. Expt. Sta., 1930a, 1930b, 1930d.
Okinawa Pref. Fish. Expt. Sta., 1940a, 1943.
Sasaki, 1939a.
Shapiro, 1948a.
Shimamura, 1927.
Shizuoka Pref. Fish. Expt. Sta., 1936, 1937.
South Seas Govt.-Gen. Fish. Expt. Sta., 1937c, 1938, 1942, 1943b.
Taihoku Prov. Fish. Expt. Sta., 1927a, 1927b, 1929, 1932.
Takayama, Ikeda, and Ando, 1934.
Uda, 1935b, 1938, 1939, 1940c.
Uehara, 1941.
Yabe and Mori, 1948.
Fishing conditions correlated with weather
Kanamura and Yazaki, 1940b.
Okinawa Pref. Fish. Expt. Sta., 1940a, 1943.
Taihoku Prov. Fish. Expt. Sta., 1927a, 1927b.
Uda and Watanabe, 1938.
Food
Clemens and Wilby, 1946.
Delsman and Hardenburg, 1934.
Eckles, 1949b.
Hatai et al., 1941.
Hildebrand, 1946.
Imamura, 1949.
Kishinouye, 1917b, 1923.
Nakamura Res. Staff, 1949.
Shapiro, 1948a.
Suyehiro, 1936, 1938, 1942.
Taihoku Prov. Fish. Expt. Sta., 1928, 1929.
Tinker, 1944.
Tominaga, 1943.
Walford, 1937.
Yabe and Mori, 1948.
Growth
Aikawa and Kato, 1938.
Habits
Imamura, 1949.
Kishinouye, 1923.
Shapiro, 1948a.
Tinker, 1944.
Tominaga, 1943.
Uchida, 1923.
Uda, 1935b, 1940a.
Uda and Tsukushi, 1934.
Hermaphroditism
Nakamura, 1935.
Hormones
Migita and Arakawa, 1948.
Oya and Takahashi, 1936.
Toyama et al., 1941.
Keys
Brock, 1949.
Delsman and Hardenburg, 1934.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.

Katsuwonus pelamis—Continued
Keys—Continued
Hildebrand, 1946.
Kishinouye, 1915a, 1923.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Okada and Matsubara, 1938.
Roedel, 1948b.
Serventy, 1941.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931, 1937.
Length-weight relation
Bonham, 1946.
Measurement data
Aikawa and Kato, 1938.
Bonham, 1946.
Godsil and Byers, 1944.
Higashi, 1940a, 1940b, 1941a, 1941b, 1942.
Ikebe and Matsumoto, 1937.
Kagoshima Pref. Fish. Expt. Sta., 1925, 1926a, 1927b, 1928a, 1929a, 1936a, 1937, 1938a, 1939a, 1940a, 1941.
Kodama, Iizuka, and Harada, 1934.
Marr, 1948.
Nakamura Res. Staff, 1949.
Ōita Pref. Fish. Expt. Sta., 1925.
Okinawa Pref. Fish. Expt. Sta., 1931.
Onodera, 1941.
Schaefer, 1948b.
South Seas Govt.-Gen. Fish. Expt. Sta., 1941d.
Suyehiro, 1936, 1938.
Taihoku Prov. Fish. Expt. Sta., 1928, 1929.
Uda, 1941.
Watanabe, N., 1941.
Yabe and Mori, 1948.
Yamamoto, 1940.
Meristic characters
Godsil and Byers, 1944.
Nakamura Res. Staff, 1949.
Migration
Hatai et al., 1941.
Imamura, 1949.
Kimura, 1941, 1942b.
Kishinouye, 1923.
Matsubara, 1943.
Matsumoto, 1937.
Sasaki, 1939a.
Shapiro, 1948a, 1948b.
Tominaga, 1943.
Uda, 1936.
Walford, 1937.
Parasites
Bennett, 1840.
Harada, 1928.
Kishinouye, 1923.
Manter, 1940.
Van Cleave, 1940.
Populations
Aikawa, 1937.
Godsil and Byers, 1944.

Katsuwonus pelamis—Continued
Populations—Continued
Imamura, 1949.
Tauchi, 1941.
Tominaga, 1943.
Uda and Tsukushi, 1934.
Reproduction
Eckles, 1949b.
Hatai et al., 1941.
Imamura, 1949.
Kishinouye, 1923.
Marr, 1948.
Schaefer, 1948c.
Schaefer and Marr, 1948a.
Shapiro, 1948b.
Walford, 1937.
Yabe and Mori, 1948.
Sex ratio
Ikebe and Matsumoto, 1937.
Marr, 1948.
Nakamura Res. Staff, 1949.
Sexual dimorphism
Hatai et al., 1941.
Sexual maturity
Hatai et al., 1941.
Marr, 1948.
Matsubara, 1943.
Matsui, 1942b.
Nakamura Res. Staff, 1949.
Okinawa Pref. Fish. Expt. Sta., 1931.
Schaefer and Marr, 1948a.
Yabe and Mori, 1948.
Size composition
Aikawa, 1937.
Aikawa and Kato, 1938.
Inanami, 1942b.
Kagoshima Pref. Fish. Expt. Sta., 1937.
Kimura, 1941.
Nakamura Res. Staff, 1949.
Okamoto, 1940.
Sasaki, 1939a.
Uda, 1935b.
Uda and Tsukushi, 1934.
Yabe and Mori, 1948.
Swimming velocity
Watanabe, N., 1941.
Synonymy
Bleeker, 1856.
Boeseman, 1947.
Evermann and Seale, 1907.
FAO, 1949.
Fish, 1948.
Fowler, 1928, 1934, 1944, 1949.
Fraser-Brunner, 1950.
Günther, 1860, 1876.
Herre, 1936.
Hildebrand, 1946.
Jenkins, 1903.
Jordan and Evermann, 1896, 1905.
Jordan, Tanaka, and Snyder, 1913.

Katsuwonus pelamis—Continued
Synonymy—Continued
Kishinouye, 1923.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Nakamura, 1939b.
Phillipps, 1927b.
Richardson, 1846.
Soldatov and Lindberg, 1930.
Tanaka, 1912, 1931.
Ulrey and Greeley, 1928.
Waite, 1907.
Tagging
Anonymous, 1939.
Fukuda and Iizuka, 1940b.
Godsil, 1938.
Kagoshima Pref. Fish. Expt. Sta., 1928a, 1936b, 1938b, 1939b, 1940b.
Matsumoto, 1937.
South Seas Govt.-Gen. Fish. Expt. Sta., 1941c.
Uda, 1936.
Young
Eckles, 1949b.
Hatai et al., 1941.
Inanami, 1942e.
Kishinouye, 1919b, 1923, 1924, 1926.
Marr, 1948.
Schaefer, 1948e.
Schaefer and Marr, 1948a.
Yabe and Mori, 1948.
Young as food of tuna
Kishinouye, 1917b.
Marukawa, 1939.
Katsuwonus pelamys. See *Katsuwonus pelamis*.
Katsuwonus vagans. See *Katsuwonus pelamis*.
Katwonus vagans. See *Katsuwonus pelamis*.
Keys
Brock, 1949.
Delsman and Hardenburg, 1934.
Fraser-Brunner, 1949, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Kishinouye, 1915a, 1923.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Nakamura, 1949.
Okada and Matsubara, 1938.
Roedel, 1948b.
Serventy, 1941.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Wade, 1949.
Walford, 1931, 1937.
Kishinoella
Keys
Soldatov and Lindberg, 1930.
Kishinoella rara
Classification
Nakamura, 1939b.
Okada and Matsubara, 1938.
Common names
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Compared with *Kishinoella zacalles*
Nakamura, 1939b.
Description
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Distribution
Jordan and Evermann, 1926a, 1926b.
Jordan and Hubbs, 1925.
Nakamura, 1939b.
Okada and Matsubara, 1938.
Figured
Nakamura, 1939b.
Keys
Brock, 1949.
Jordan and Evermann, 1926b.
Okada and Matsubara, 1938.
Synonymy
Nakamura, 1939b.
Kishinoella tonggol
Anatomy
Serventy, 1942b.
Common names
Serventy, 1941.
Whitley, 1947.
Compared with *Kishinoella zacalles*
Serventy, 1942b.
Compared with *Neothunnus rarus*
Serventy, 1942b.
Compared with *Thunnus maccoyi*
Serventy, 1941.
Compared with *Thunnus nicolsoni*
Serventy, 1942b.
Compared with *Thunnus tonggol*
Serventy, 1942b.
Description
Serventy, 1941, 1942b.
Distribution
Serventy, 1941, 1942a, 1942b.
Whitley, 1947.
Figured
Serventy, 1941, 1942b.
Food
Serventy, 1942a.
Habits
Serventy, 1942a.
Keys
Serventy, 1941.
Length-weight relation
Serventy, 1941.

Kishinoella tonggol—Continued
Measurement data
Serventy, 1942b.
Reproduction
Serventy, 1942a.
Synonymy
Serventy, 1942b.
Kishinoella zacalles
Classification
Fraser-Brunner, 1950.
Nichols and LaMonte, 1941.
Compared with *Kishinoella rara*
Nakamura, 1939b.
Compared with *Kishinoella tonggol*
Serventy, 1942b.
Description
Fraser-Brunner, 1950.
Jordan and Evermann, 1926b.
Distribution
Fraser-Brunner, 1950.
Jordan and Evermann, 1926b.
Figured
Fraser-Brunner, 1950.
Jordan and Evermann, 1926b.
Keys
Fraser-Brunner, 1950.
Jordan and Evermann, 1926b.
Synonymy
Fraser-Brunner, 1950.

Length-weight data. See Morphometrics.

Mackerel, frigate. See *Auxis* spp.
Management
Schaefer, 1948c.
Maturity
Anonymous, 1938.
Ban, 1941.
Clark, 1929.
Hatai et al., 1941.
Ikebe, 1939.
Imaizumi, 1937.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Kato, 1940.
Marr, 1948.
Matsubara, 1943.
Matsui, 1942b.
Nakamura, 1938.
Nakamura Res. Staff, 1949.
Okinawa Pref. Fish. Expt. Sta., 1931.
Okuma, Imaizumi, and Maki, 1935.
Schaefer, 1948b.
Schaefer and Marr, 1948a.
Soc. Prom. Ocean. Fish., 1936.
Watanabe, H., 1939.
Measurement data. See Morphometrics.
Migration.
Cobb, 1919.
Hatai et al., 1941.
Migration—Continued
Imamura, 1949.
Kimura, 1941, 1942b.
Kishinouye, 1923.
Kōchi Pref. Fish. Expt. Sta., 1923b, 1924.
Matsubara, 1943.
Matsumoto, 1937.
Nakamura, 1943, 1949.
Sasaki, 1939a, 1939b.
Serventy, 1941.
Shapiro, 1948a, 1948b.
Soc. Prom. Ocean. Fish., 1936.
Tauchi, 1940b.
Tominaga, 1943.
Uda, 1936.
Walford, 1937.
Whitehead, 1931.
Morphometrics
Length-weight relation
Bonham, 1946.
Hiratsuka and Morita, 1935.
Schaefer, 1948a.
Serventy, 1941.
Measurement data
Aikawa and Kato, 1938.
Anonymous, 1938.
Bonham, 1946.
Brock, 1943, 1949.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Godsil, 1948.
Godsil and Byers, 1944.
Higashi, 1940a, 1940b, 1941a, 1941c, 1942.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Ikebe, 1939, 1940a, 1940b, 1940c, 1941a, 1941b.
Ikebe and Matsumoto, 1937.
Inanami, 1940a.
Japanese Bur. Fish., 1939, 1940.
Kagoshima Pref. Fish. Expt. Sta., 1925, 1926a, 1927b, 1928a, 1929a, 1936a, 1937, 1938a, 1939a, 1940a, 1941.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Kodama, Iizuka, and Harada, 1934.
Marr, 1948.
Miyama, Sarnya, and Hasegawa, 1939.
Nakamura, 1936, 1939a, 1939b.
Nakamura Res. Staff, 1949.
Ōita Pref. Fish. Expt. Sta., 1925, 1927a, 1927b, 1930.
Okinawa Pref. Fish. Expt. Sta., 1931.
Okuma, Imaizumi, and Maki, 1935.
Onodera, 1941.
Schaefer, 1948a, 1948b.
Serventy, 1942b, 1948.
South Seas Govt.-Gen. Fish. Expt. Sta., 1941d, 1943a.
Suyehiro, 1936, 1938.
Taihoku Prov. Fish. Expt. Sta., 1928, 1929.
Uda, 1932, 1941.
Uno, 1936b.
Wade, 1949.
Watanabe, Hajime, 1939.

Morphometrics—Continued
Measurement data—Continued
Watanabe, Haruo, 1940.
Watanabe, N., 1941.
Yabe and Mori, 1948.
Yamamoto, 1940.
Meristic characters
Clark, 1929.
Godsil and Byers, 1944.
Nakamura Res. Staff, 1949.
Schaefer and Marr, 1948b.
Wade, 1949.
Methods of measurement
Godsil, 1948.
Godsil and Byers, 1944.
Marr and Schaefer, 1949.
Sex ratio
Brock, 1943.
Ikebe and Matsumoto, 1937.
Marr, 1948.
Miyama, Saruya, and Hasegawa, 1939.
Nakamura Res. Staff, 1949.

Neothunnus
Compared with *Semathunnus*
Fowler, 1933.
Nakamura, 1939a.
New species recorded
Jordan and Evermann, 1926a.
Neothunnus albacora
Classification
Nichols and LaMonte, 1941.
Common names
Nichols and LaMonte, 1941.
Description
Nichols and LaMonte, 1941.
Keys
Nichols and LaMonte, 1941.
Synonymy
Nichols and LaMonte, 1941.
Neothunnus albacora albacora. See *Neothunnus albacora.*
Neothunnus albacora macropterus. See *Neothunnus macropterus.*
Neothunnus allisoni
Classification
Nichols and LaMonte, 1941.
Common names
Nichols and LaMonte, 1941.
Compared with *Neothunnus macropterus*
Walford, 1937.
Description
Nichols and LaMonte, 1941.
Keys
Nichols and LaMonte, 1941.
Synonymy
Nichols and LaMonte, 1941.
Neothunnus allisoni allisoni. See *Neothunnus allisoni.*
Neothunnus allisoni itosibi. See *Neothunnus itosibi.*
Neothunnus argentivittatus
Common names
Nichols and Murphy, 1922.
Description
Nichols and Murphy, 1922.
Distribution
Fowler, 1944.
Jordan and Jordan, 1922.
Nichols and Murphy, 1922.
Neothunnus catalinae
Classification
Nichols and LaMonte, 1941.
Common names
Craig, 1929.
Nichols and LaMonte, 1941.
Description
Jordan and Evermann, 1926b.
Nichols and LaMonte, 1941.
Distribution
Jordan and Evermann, 1926b.
Ulrey, 1929.
Figured
Jordan and Evermann, 1926b.
Keys
Jordan and Evermann, 1926b.
Nichols and LaMonte, 1941.
Synonymy
Nichols and LaMonte, 1941.
Neothunnus itosibi
Classification
Nichols and LaMonte, 1941.
Okada and Matsubara, 1938.
Common names
Jordan and Evermann, 1926b.
Okada and Matsubara, 1938.
Compared with *Neothunnus macropterus*
Nakamura, 1939a, 1939b.
Description
Fowler, 1928.
Jordan and Evermann, 1926b.
Okada and Matsubara, 1938.
Powell, 1937.
Distribution
Domantay, 1940.
Fowler, 1928.
Jordan and Evermann, 1926b.
Martin, 1938.
Okada and Matsubara, 1938.
Powell, 1937.
Figured
Domantay, 1940.
Jordan and Evermann, 1926b.
Powell, 1937.
Keys
Jordan and Evermann, 1926b.
Okada and Matsubara, 1938.
Synonymy
Fowler, 1928.
Powell, 1937.

Neothunnus macropterus
Age
Aikawa and Kato, 1938.
Ban, 1941.
Higashi, 1941b.
Ikebe, 1939, 1940a, 1940b, 1940c, 1941a, 1941b.
Kanamura and Yazaki, 1940a, 1940b.
Kimura, 1942a.
Schaefer, 1948b.
Tauchi, 1940b.
Anatomy
Fish, 1948.
Godsil and Byers, 1944.
Higashi, 1941c.
Kishinouye, 1915a, 1915b, 1919a, 1922a, 1923.
Matsui, 1942a.
Migita and Arakawa, 1948.
Nakamura, 1949.
Snyehiro, 1941, 1942.
Body condition
Aikawa and Kato, 1938.
Ikebe, 1939.
Kanamura and Yazaki, 1940a, 1940b.
Body temperature
Anonymous, 1938.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Nakamura, 1941.
Ōita Pref. Fish. Expt. Sta., 1927a, 1930.
Catch per unit of effort
Formosa Govt.-Gen. Fish Expt. Sta., 1933a.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Imaizumi, 1937.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Nakamura, 1949.
Okuma, Imaizumi, and Maki, 1935.
Chemical analysis
Dill, 1921.
Higashi and Hirai, 1948.
Miyama and Osakabe, 1940.
Miyama, Saruya, and Hasegawa, 1939.
Classification
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Kishinouye, 1915a, 1923.
Nakamura, 1939a, 1939b, 1943, 1949.
Nichols and LaMonte, 1941.
Okada and Matsubara, 1938.
Roedel, 1948b.
Schaefer, 1948a
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931.
Common names
Barnhart, 1936.
Delsman and Hardenburg, 1934.

Neothunnus macropterus—Continued
Common names—Continued
FAO, 1949.
Fish, 1948.
Fujita and Wakiya, 1915.
Herre and Umali, 1948.
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Jordan and Snyder, 1901.
Jordan, Tanaka, and Snyder, 1913.
Kishinouye, 1915a, 1923.
Kumata et al., 1941.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a, 1948b.
Smith, 1947.
Starks and Morris, 1907.
Tinker, 1944.
Ulrey and Greeley, 1928.
Walford, 1931, 1937.
Whitley, 1947.
Compared with *Neothunnus allisoni*
Walford, 1937.
Compared with *Neothunnus itosibi*
Nakamura, 1939a, 1939b.
Compared with *Parathunnus mebachi*
Roedel, 1948b.
Compared with *Scmathunnus guildi*
Nakamura, 1939b.
Compared with *Thunnus thynnus*
Thompson and Higgins, 1919.
Description
Barnhart, 1936.
Boeseman, 1947.
Delsman and Hardenburg, 1934.
Fowler, 1928.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Jordan and Starks, 1907.
Kishinouye, 1915a, 1923.
Matsubara, 1943.
Nakamura, 1939b, 1949.
Okada and Matsubara, 1938.
Roedel, 1948b.
Seale, 1940.
Serventy, 1941.
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Starks, 1918.
Temminck and Schlegel, 1850.
Thompson and Higgins, 1919.
Tinker, 1944.
Walford, 1931, 1937.

Neothunnus macropterus—Continued
Distribution
Abe, 1939.
Anonymous, 1938.
Barnhart, 1936.
Bleeker, 1852, 1862, 1865a.
Chapman, 1946.
Chu, 1931.
Delsman and Hardenburg, 1934.
Domantay, 1940.
Eckles, 1949a.
FAO, 1949.
Fish, 1948.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Fowler, 1923a, 1928, 1931, 1938, 1949.
Fraser-Brunner, 1950.
Fujita and Wakiya, 1915.
Godsil and Greenhood, 1948.
Herre, 1932, 1935, 1936, 1940.
Hildebrand, 1946.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Holder, 1912.
Hubbs, 1916.
Imaizumi, 1937.
Japanese Bur. Fish., 1934.
Jordan and Evermann, 1926a, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Jordan and Seale, 1906.
Jordan and Snyder, 1901.
Jordan and Starks, 1907.
Jordan, Tanaka, and Snyder, 1913.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Kimura, 1942b.
Kishinouye, 1915a, 1923.
Kōchi Pref. Fish. Expt. Sta., 1923b, -924.
Kumata et al., 1941.
Martin, 1938.
Matsubara, 1943.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Okuma, Imaizumi, and Maki, 1935.
Reeves, 1928.
Richardson, 1846.
Roedel, 1948b.
Schaefer, 1948c.
Seale, 1940.
Serventy, 1941.
Shapiro, 1948a, 1948b.
Smith and Schaefer, 1949.
Soldatov and Lindberg, 1930.
South Seas Govt.-Gen. Fish. Expt. Sta., 1937a.
Starks, 1918.
Starks and Morris, 1907.
Takao Prov. Fish. Expt. Sta., 1927.
Tanaka, 1931.
Taranetz, 1937.
Temminck and Schlegel, 1850.

Neothunnus macropterus—Continued
Distribution—Continued
Tinker, 1944.
Ulrey, 1929.
Ulrey and Greeley, 1928.
Walford, 1931, 1937.
Whitley, 1928, 1947.
Distribution correlated with water temperature
Takayama and Ando, 1934.
Uda, 1935a.
Exploitation rates
Tauchi, 1940b.
Figured
Anonymous, 1938.
Barnhart, 1936.
Delsman and Hardenburg, 1934.
Domantay, 1940.
Eckles, 1949a.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Jordan and Evermann, 1926b.
Jordan and Starks, 1907.
Kishinouye, 1915a, 1923.
Kitahara, 1897.
Kumata et al., 1941.
Nakamura, 1949.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a.
Starks, 1918.
Temminck and Schlegel, 1850.
Tinker, 1944.
Walford, 1931, 1937.
Fishing conditions correlated with astronomical phenomena
Takao Prov. Fish. Expt. Sta., 1927.
Fishing conditions correlated with oceanography
Aikawa, 1933.
Ban, 1941.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Ikebe, 1940d, 1942.
Inanami, 1940b, 1940c, 1941, 1942d.
Japanese Bur. Fish., 1934.
Kagoshima Pref. Fish. Expt. Sta., 1926b, 1927a, 1928b, 1929b, 1930b, 1930c, 1931b, 1932b, 1933b.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Kawamura, 1939.
Kimura, 1942a.
Kimura and Ishii, 1933.
Mie Pref. Fish. Expt. Sta., 1930c, 1930e.
Nakamura, 1949.
Ōita Pref. Fish. Expt. Sta., 1930.
Okuma, Imaizumi, and Maki, 1935.
Shapiro, 1948a.
South Seas Govt.-Gen. Fish. Expt. Sta., 1937a, 1938, 1941b, 1942, 1943b.
Takao Prov. Fish Expt. Sta., 1927.

Neothunnus macropterus—Continued
Fishing conditions correlated with oceanography—Con.
Takayama and Ando, 1934.
Uehara, 1941.
Fishing conditions correlated with weather
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Kanamura and Yazaki, 1940a, 1940b.
Ōita Pref. Fish. Expt. Sta., 1930.
Okuma, Imaizumi, and Maki, 1935.
Food
Anonymous, 1938.
Ban, 1941.
Chapman, 1946.
Fitch, 1950.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Herald, 1949.
Hildebrand, 1946.
Japanese Bur. Fish., 1934.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Kishinouye, 1917b, 1923.
Marukawa, 1939.
Miyama, Saruya, and Hasegawa, 1939.
Nakamura, 1936, 1943, 1949.
Okuma, Imaizumi, and Maki, 1935.
Shapiro, 1948a.
Suyehiro, 1942.
Tinker, 1944.
Walford, 1937.
Growth
Aikawa and Kato, 1938.
Kimura, 1932, 1935.
Kishinouye, 1923.
Schaefer, 1948a, 1948b.
Habits
Kishinouye, 1923.
Nakamura, 1949.
Schaefer, 1948b.
Shapiro, 1948a.
Hormones
Migita and Arakawa, 1948.
Toyama et al., 1941.
Keys
Brock, 1949.
Delsman and Hardenburg, 1934.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Jordan and Evermann, 1926b.
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Okada and Matsubara, 1938.
Roedel, 1948b.
Serventy, 1941.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931, 1937.

Neothunnus macropterus—Continued
Length-weight relation
Hiratsuka and Morita, 1935
Schaefer, 1948a.
Measurement data
Aikawa and Kato, 1938.
Anonymous, 1938.
Bonham, 1946.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Godsil, 1948.
Godsil and Byers, 1944.
Higashi, 1940a, 1941b, 1941c, 1942.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Ikebe, 1939, 1940a, 1940b, 1940c, 1941a, 1941b.
Inanami, 1940a.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a, 1940b.
Marr, 1948.
Miyama, Saruya, and Hasegawa, 1939.
Nakamura, 1936, 1939a, 1939b.
Ōita Pref. Fish. Expt. Sta., 1925, 1927a, 1927b, 1930.
Okuma, Imaizumi, and Maki, 1935.
Schaefer, 1948a, 1948b.
South Seas Govt.-Gen. Fish. Expt. Sta., 1943a.
Watanabe, H., 1940.
Meristic characters
Godsil and Byers, 1944.
Migration
Kōchi Pref. Fish. Expt. Sta., 1923b, 1924.
Nakamura, 1943.
Shapiro, 1948a.
Tauchi, 1940b.
Walford, 1937.
Parasites
Kishinouye, 1923.
Populations
Godsil, 1948, 1949.
Godsil and Byers, 1944.
Tauchi, 1940b.
Reproduction
Hatai et al., 1941.
Ikebe, 1941b.
Kishinouye, 1923.
Marr, 1948.
Nakamura, 1939b, 1943, 1949.
Schaefer, 1948c.
Schaefer and Marr, 1948a.
Tinker, 1944.
Walford, 1937.
Sex ratio
Marr, 1948.
Miyama, Saruya, and Hasegawa, 1939.
Sexual maturity
Anonymous, 1938.
Ban, 1941.
Hatai et al., 1941.
Ikebe, 1939.
Imaizumi, 1937.
Kanamura and Imaizumi, 1935.

Neothunnus macropterus—Continued
Sexual maturity—Continued
Kanamura and Yazaki, 1940a, 1940b.
Kato, 1940.
Marr, 1948.
Okuma, Imaizumi, and Maki, 1935.
Schaefer, 1948b.
Schaefer and Marr, 1948a.
Size composition
Aikawa and Kato, 1938.
Kimura, 1932, 1942a.
Schaefer, 1948b.
Schaefer and Marr, 1948a.
Tauchi, 1940b.
Survival rates
Tauchi, 1940b.
Synonymy
Boeseman, 1947.
Chu, 1931.
FAO, 1949.
Fish, 1948.
Fowler, 1928, 1931, 1949.
Fraser-Brunner, 1950.
Herre, 1936.
Hildebrand, 1946.
Jordan and Hubbs, 1925.
Jordan and Starks, 1907.
Jordan, Tanaka, and Snyder, 1913.
Kishinouye, 1923.
Nakamura, 1939a, 1939b, 1949.
Richardson, 1846.
Soldatov and Lindberg, 1930.
Tanaka, 1931.
Ulrey and Greeley, 1928.
Tagging
Godsil, 1938.
Young
Kishinouye, 1924, 1926.
Schaefer, 1948c.
Schaefer and Marr, 1948a.
Neothunnus rarus
Anatomy
Kishinouye, 1915a, 1915b, 1923.
Nakamura, 1949.
Classification
Kishinouye, 1915a, 1923.
Nakamura, 1943, 1949.
Nichols and LaMonte, 1941.
Common names
Delsman and Hardenburg, 1934.
Kishinouye, 1915a, 1923.
Nakamura, 1943, 1949.
Nichols and LaMonte, 1941.
Compared with *Kishinoella tonggol*
Serventy, 1942b.
Description
Delsman and Hardenburg, 1934.
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Nichols and LaMonte, 1941.
Neothunnus rarus—Continued
Distribution
Delsman and Hardenburg, 1934.
Herre, 1940.
Kishinouye, 1915a, 1923.
Nakamura, 1943, 1949.
Eggs
Delsman and Hardenburg, 1934.
Figured
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Food
Kishinouye, 1923.
Nakamura, 1943, 1949.
Habits
Kishinouye, 1923.
Nakamura, 1949.
Keys
Delsman and Hardenburg, 1934.
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Nichols and LaMonte, 1941.
Migration
Nakamura, 1943.
Reproduction
Delsman and Hardenburg, 1934.
Nakamura, 1943.
Synonymy
Kishinouye, 1923.
Nakamura, 1949.
Nichols and LaMonte, 1941.
Neothunnus rarus zacalles. See *Kishinoella zacalles.*
Neothunnus tonggol
Description
Jordan and Evermann, 1926b.
Distribution
Jordan and Evermann, 1926b.
Keys
Jordan and Evermann, 1926b.
Synonymy
Jordan and Evermann, 1926b.
Neothynnus macropterus. See *Neothunnus macropterus.*
Nicotinic acid
Higashi and Hirai, 1948.
Nomenclature, tuna. See Tuna, common names.

Oceanographic conditions. See also Currents; Salinity; Specific gravity; Tides; Water.
Correlated with fishing
Ban, 1941.
Formosa Govt.-Gen. Fish. Expt. Sta., 1933a.
Hiratsuka and Imaizumi, 1934.
Hiratsuka and Ito, 1934.
Ikehe, 1942.
Imamura, 1949.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940b.
Kawamura, 1939.
Kōchi Pref. Fish. Expt. Sta., 1923a.
Nakamura, 1949.

Oceanographic conditions—Continued
Correlated with fishing—Continued
Ōita Pref. Fish. Expt. Sta., 1930.
Okuma, Imaizumi, and Maki, 1935.
Scagel, 1949.
Shapiro, 1948a.
South Seas Govt.-Gen. Fish. Expt. Sta., 1937c, 1938, 1941b.
Taihoku Prov. Fish. Expt. Sta., 1927a, 1927b.
Uda, 1935b, 1940c.
Correlated with location of fishing grounds
Inanami, 1942a.
Soc. Prom. Ocean. Fish., 1936.
Orcynus. See Thunnidae.
Orcynus alalonga. See *Thunnus germo*.
Orcynus germo. See *Thunnus germo*.
Orcynus pacificus. See *Thunnus germo*.

Parasites
Bennett, 1840.
Harada, 1928.
Kishinouye, 1923.
Manter, 1940.
Van Cleave, 1940.
Parathunnus
Keys
Soldatov and Lindberg, 1930.
Parathunnus mebachi
Anatomy
Godsil and Byers, 1944.
Higashi, 1941c.
Kishinouye, 1915a, 1915b, 1918, 1919a, 1922a, 1923.
Nakamura, 1949.
Body temperature
Kanamura and Imaizumi, 1935.
Ōita Pref. Fish. Expt. Sta., 1927a, 1930.
Catch per unit of effort
Imaizumi, 1937.
Japanese Bur. Fish., 1939.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a.
Nakamura, 1949.
Chemical analysis
Miyama and Osakabe, 1940.
Miyauchi, 1915.
Classification
Godsil and Byers, 1944.
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1943, 1949.
Common names
Kishinouye, 1915a, 1923.
Kumata et al., 1941.
Nakamura, 1939b, 1943, 1949.
Compared with *Neothunnus macropterus*
Roedel, 1948b.
Compared with *Thunnus germo*
Roedel, 1948b.
Description
Godsil and Byers, 1944.
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1949.
Parathunnus mebachi—Continued
Distribution
Fish, 1948.
Imaiznmi, 1937.
Japanese Bur. Fish., 1934.
Kanamura and Imaizumi, 1935.
Kanamura and Yazaki, 1940a.
Kimura, 1942b.
Kishinouye, 1915a, 1923.
Kōchi Pref. Fish. Expt. Sta., 1923b, 1924.
Kumata et al., 1941.
Matsubara, 1943.
Nakamura, 1939b, 1943, 1949.
Takao Prov. Fish. Expt. Sta., 1927.
Distribution correlated with water temperatures
Takayama and Ando, 1934.
Figured
Godsil and Byers, 1944.
Kishinouye, 1915a, 1923.
Kumata et al., 1941.
Nakamura, 1949.
Fishing conditions correlated with astronomical phenomena
Takao Prov. Fish. Expt. Sta., 1927.
Fishing conditions correlated with oceanography
Aikawa, 1933.
Fukuda and Iizuka, 1940a.
Ikebe, 1942.
Inanami, 1940b, 1940c, 1942d.
Japanese Bur. Fish., 1934, 1939.
Kagoshima Pref. Fish. Expt. Sta., 1926b, 1927a, 1928b, 1929b, 1930b, 1930c, 1931b, 1932b, 1933b.
Kanamura and Imaizumi, 1935.
Kimura, 1942a.
Mie Pref. Fish. Expt. Sta., 1930c, 1930e.
Nakamura, 1949.
Ōita Pref. Fish Expt. Sta., 1930.
Okinawa Pref. Fish. Expt. Sta., 1940b.
Ōmori and Fujimoto, 1940.
Ōmori and Fukuda, 1938, 1940.
South Seas Govt.-Gen. Fish. Expt. Sta., 1942.
Takao Prov. Fish. Expt. Sta., 1927.
Takayama and Ando, 1934.
Uehara, 1941.
Fishing conditions correlated with weather
Kanamura and Imaizumi, 1935.
Ōita Pref. Fish. Expt. Sta., 1930.
Food
Kishinouye, 1917b, 1923.
Nakamura, 1943, 1949.
Habits
Kishinouye, 1923.
Nakamura, 1949.
Keys
Godsil and Byers, 1944.
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Measurement data
Godsil and Byers, 1944.
Higashi, 1940a, 1941c.

Parathunnus mebachi—Continued
Measurement data—Continued
Ikebe, 1940a.
Kanamura and Imaizumi, 1935.
Ōita Pref. Fish. Expt. Sta., 1925, 1927a, 1927b, 1930.
Watanabe, H., 1940.
Meristic characters
Godsil and Byers, 1944.
Migration
Kōchi Pref. Fish. Expt. Sta., 1923b, 1924.
Nakamura, 1943.
Parasites
Kishinouye, 1923.
Reproduction
Nakamura, 1943.
Sexual maturity
Kanamura and Imaizumi, 1935.
Synonymy
Kishinouye, 1923.
Nakamura, 1939b, 1949.
Young
Hatai et al., 1941.
Kishinouye, 1926.
Young as food of tunas
Kishinouye, 1917b.
Parathunnus sibi
Anatomy
Suyehiro, 1941, 1942.
Chemical analysis
Miyama and Osakabe, 1938.
Classification
Okada and Matsubara, 1938.
Common names
Jordan and Hubbs, 1925.
Jordan and Snyder, 1901.
Okada and Matsubara, 1938.
Shapiro, 1948b.
Tinker, 1944.
Ulrey and Greeley, 1928.
Compared with *Pelamys sibi*
Bleeker, 1879.
Compared with *Thynnus alalonga*
Temminck and Schlegel, 1850.
Description
Brock, 1949.
Fowler, 1927, 1928.
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Okada and Matsubara, 1938.
Temminck and Schlegel, 1850.
Tinker, 1944.
Distribution
Domantay, 1940.
Fowler, 1927, 1928, 1929, 1931, 1938, 1949.
Herre, 1940.
Jordan and Evermann, 1926a, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Jordan and Snyder, 1901.
Parathunnus sibi—Continued
Distribution—Continued
Okada and Matsubara, 1938.
Richardson, 1846.
Shapiro, 1948b.
Smith and Schaefer, 1949.
Snyder, 1904.
Tanaka, 1931.
Tinker, 1944.
Ulrey, 1929.
Ulrey and Greeley, 1928.
Distribution correlated with water temperature
Uda, 1935a.
Figured
Domantay, 1940.
Fowler, 1927, 1928.
Jordan and Evermann, 1926b.
Kitahara, 1897.
Temminck and Schlegel, 1850.
Tinker, 1944.
Food
Suyehiro, 1942.
Habits
Brock, 1949.
Hormones
Toyama et al., 1941.
Keys
Brock, 1949.
Jordan and Evermann, 1926b.
Okada and Matsubara, 1938.
Measurement data
Brock, 1949.
Higashi, 1942.
Synonymy
Fowler, 1928, 1949.
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Richardson, 1846.
Tanaka, 1931.
Ulrey and Greeley, 1928.
Young as food of tunas
Marukawa, 1939.
Parathynnus sibi. See *Parathunnus sibi.*
Pelamys affine. See *Euthynnus alletteratus.*
Pelamys macropterus. See *Neothunnus macropterus.*
Pelamys pelamys. See *Katsuwonus pelamis.*
Pelamys sibi
Compared with *Thynnus sibi*
Bleeker, 1879.
Pelamys thunnina. See *Euthynnus alletteratus.*
Plecostei
Anatomy
Berg, 1947.
Kishinouye, 1917a.
Takahashi, 1924.
Classification
Berg, 1947.
Kishinouye, 1917a.
Takahashi, 1924, 1926.

Populations
Aikawa, 1937.
Brock, 1943.
Clark, 1929.
Godsil, 1948, 1949.
Godsil and Byers, 1944.
Imamura, 1949.
Tauchi, 1940a, 1940b, 1940c, 1941.
Tominaga, 1943.
Uda and Tokunaga, 1937.
Uda and Tsukushi, 1934.

Reproduction
Brock, 1943.
Delsman and Hardenburg, 1934.
Eckles, 1949b.
Hatai et al., 1941.
Ikehe, 1941b.
Imamura, 1949.
Kishinouye, 1915a, 1923.
Marr, 1948.
Nakamura, 1938, 1939b, 1943, 1949.
Schaefer, 1948c.
Schaefer and Marr, 1948a.
Serventy, 1941, 1942a.
Shapiro, 1948b.
Soc. Prom. Ocean. Fish., 1936.
Tinker, 1944.
Walford, 1937.
Watanabe, H., 1939.
Whitehead, 1931.
Yabe and Mori, 1948.

Salinity. See also Oceanographic conditions.
Correlated with fishing
Inanami, 1941.
Uda and Tokunaga, 1937.
Scomber taso. See *Auxis taso*.
Semathunnus
Compared with *Neothunnus*
Fowler, 1933.
Nakamura, 1939a.
Semathunnus guildi
Compared with *Neothunnus macropterus*
Nakamura, 1939b.
Description
Fowler, 1933.
Distribution
Fowler, 1934.
Synonymy
Fowler, 1934.
Semathunnus itosibi
Common names
Tinker, 1944.
Description
Tinker, 1944.
Distribution
Fowler, 1934.
Tinker, 1944.
Synonymy
Fowler, 1934.

Sex. See Morphometrics.
Sexual maturity. See Maturity.
Size composition
Aikawa, 1937.
Aikawa and Kato, 1938.
Brock, 1943.
Hart et al., 1948.
Inanami, 1942b.
Kagoshima Pref. Fish. Expt. Sta., 1937.
Kawana, 1934.
Kida, 1936.
Kimura, 1932, 1935, 1941, 1942a.
Mine and Iehisa, 1940.
Nakamura Res. Staff, 1949.
Okamoto, 1940.
Sasaki, 1939a, 1939b.
Seagel, 1949.
Schaefer, 1948b.
Schaefer and Marr, 1948a.
Serventy, 1941, 1947.
Tauchi, 1940a, 1940b, 1940c.
Uda, 1935b.
Uda and Tsukushi, 1934.
Yabe and Mori, 1948.
Skipjack. See *Katsuwonus pelamis*.
Skipjack, black. See *Euthynnus* spp.
Spawning. See Reproduction.
Specific gravity
Correlated with fishing
Formosa Govt.–Gen. Fish. Expt. Sta., 1930, 1931, 1932, 1933b, 1934.
Japanese Bur. Fish., 1939, 1940.
Mie Pref. Fish. Expt. Sta., 1930a, 1930b, 1930c, 1930d, 1930e.
Ōmori and Fujimoto, 1940.
Ōmori and Fukuda, 1938, 1940.
Shimamura, 1927.
Taihoku Prov. Fish. Expt. Sta., 1929.
Stock. See Populations.
Stomach contents. See Food.
Survival rates
Tauchi, 1940a, 1940b, 1940c.
Synonymy
Bleeker, 1852, 1856.
Boeseman, 1947.
Chevey, 1932a, 1934.
Chu, 1931.
Evermann and Seale, 1907.
FAO, 1949.
Fish, 1948.
Fowler, 1904b, 1928, 1931, 1934, 1938, 1944, 1949.
Fraser-Brunner, 1949, 1950.
Griffin, 1927.
Günther, 1860, 1876.
Herre, 1936.
Hildebrand, 1946.
Jenkins, 1903.
Jordan, 1923.
Jordan and Evermann, 1896, 1905, 1926b.
Jordan and Gilbert, 1882.

Synonymy—Continued
Jordan and Hubbs, 1925.
Jordan and Starks, 1907.
Jordan, Tanaka, and Snyder, 1913.
Kishinouye, 1923.
Lütken, 1880.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Nakamura, 1939a, 1939b, 1949.
Nichols and LaMonte, 1941.
Phillipps, 1927b.
Powell, 1937.
Richardson, 1846.
Schultz, 1949.
Schultz and DeLacy, 1936.
Serventy, 1942b.
Soldatov and Lindberg, 1930.
Tanaka, 1912, 1931.
Ulrey and Greeley, 1928.
Wade, 1949.
Waite, 1907, 1921.
Weber, 1913,
Whitley, 1937.

Tagging
Anonymous, 1939.
Fukuda and Iizuka, 1940b.
Godsil, 1938.
Kagoshima Pref. Fish. Expt. Sta., 1928a, 1936b, 1938b, 1939b, 1940b.
Kawana, 1934.
Matsumoto, 1937.
Scagel, 1949.
South Seas Govt.-Gen. Fish. Expt. Sta., 1941c.
Uda, 1936.
Temperature. See Body temperature; Water temperature; also Oceanographic conditions.
Thunnidae
Anatomy
Kishinouye, 1917a, 1919a.
Classification
Jordan, 1923.
Kishinouye, 1917a.
Lütken, 1880.
Distribution
Bleeker, 1844.
Keys
Jordan and Hubbs, 1925.
Synonymy
Jordan, 1923.
Lütken, 1880.
Thunniformes. See Plecostei.
Thunnus alalunga. See *Thunnus germo*.
Thunnus albacora. See *Neothunnus macropterus*.
Thunnus germo
Age
Aikawa and Kato, 1938.
Brock, 1943.
Ikebe, 1940c.
Kanamura and Yazaki, 1940b.
Kimura, 1942a.
Thunnus germo—Continued
Age—Continued
Tauchi, 1940c.
Uno, 1936b.
Anatomy
Bennett, 1840.
Fish, 1948.
Godsil and Byers, 1944.
Kishinouye, 1915a, 1915b, 1919a, 1922a, 1923.
Nakamura, 1949.
Suyehiro, 1941.
Body condition
Aikawa and Kato, 1938.
Kanamura and Yazaki, 1940b.
Soc. Prom. Ocean. Fish., 1936.
Body temperature
Anonymous, 1938.
Kanamura and Yazaki, 1940b.
Ōita Pref. Fish. Expt. Sta., 1927a.
Scagel, 1949.
Catch per unit of effort
Imaizumi, 1937.
Japanese Bur. Fish., 1939, 1940.
Kanamura and Yazaki, 1940a, 1940b.
Nakamura, 1949.
Chemical analysis
Dill, 1921.
Miyauchi, 1915.
Soc. Prom. Ocean. Fish., 1936.
Classification
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Phillipps, 1927b.
Roedel, 1948b.
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931.
Common names
Barnhart, 1936.
Craig, 1929.
FAO, 1949.
Fish, 1948.
Fujita and Wakiya, 1915.
Herre and Umali, 1948.
Jordan and Evermann, 1896, 1905.
Jordan and Hubbs, 1925.
Jordan, Tanaka, and Snyder, 1913.
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Phillipps, 1927b.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a, 1948b.
Smith, 1947.
Starks and Morris, 1907.

Thunnus germo—Continued
Common names—Continued
Tinker, 1944.
Ulrey and Greeley, 1928.
Walford, 1931, 1937.
Compared with *Parathunnus mebachi*
Roedel, 1948b.
Description
Barnhart, 1936.
Bennett, 1840.
Boeseman, 1947.
Clemens and Wilby, 1946.
Cooper, 1863.
Cuvier and Valenciennes, 1831.
Fowler, 1904b, 1928.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Griffin, 1927.
Günther, 1860, 1876.
Jordan and Evermann, 1905, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Kishinouye, 1915a, 1923.
Meek and Hildebrand, 1923.
Nakamura, 1939b, 1949.
Okada and Matsubara, 1938.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a.
Soldatov and Lindberg, 1930.
Starks, 1918.
Stead, 1906.
Tinker, 1944.
Walford, 1931, 1937.
Distribution
Anonymous, 1938.
Barnhart, 1936.
Brock, 1939.
Clemens and Wilby, 1946.
Cooper, 1863.
Cowan, 1938.
Cuvier and Valenciennes, 1831.
Eigenmann, 1892.
Eigenmann and Eigenmann, 1891.
FAO, 1949.
Fish, 1948.
Fowler, 1904a, 1923b, 1928, 1931, 1938, 1944.
Fraser-Brunner, 1950.
Fujita and Wakiya, 1915.
Gilbert and Starks, 1904.
Godsil and Greenhood, 1948.
Griffin, 1927.
Günther, 1860, 1876.
Herre, 1940.
Hildebrand, 1946.
Holder, 1912.
Hubbs, 1928.
Imaizumi, 1937.
Japanese Bur. Fish., 1939, 1940.
Jordan, 1885.

Thunnus germo—Continued
Distribution—Continued
Jordan and Evermann, 1896, 1905, 1926a, 1926b.
Jordan and Gilbert, 1881a, 1882.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Jordan and Seale, 1906.
Jordan, Tanaka, and Snyder, 1913.
Kanamura and Yazaki, 1940b.
Kimura, 1942b.
Kishinouye, 1915a, 1923.
Kōchi Pref. Fish. Expt. Sta., 1923b, 1924.
Matsubara, 1943.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Metz, 1912.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Phillipps, 1927a, 1927b.
Phillipps and Hodgkinson, 1922.
Roedel, 1948b.
Roughly, 1916.
Sampson, 1940.
Schaefer, 1948c.
Schultz and DeLaey, 1936.
Serventy, 1941, 1947.
Shapiro, 1948a, 1948b.
Soldatov and Lindberg, 1930.
Starks, 1918.
Starks and Morris, 1907.
Stead, 1906, 1908.
Tanaka, 1931.
Taranetz, 1937.
Thompson and Higgins, 1919.
Tinker, 1944.
Ulrey, 1929.
Ulrey and Greeley, 1928.
Walford, 1931, 1937.
Whitehead, 1929.
Distribution correlated with water temperature
Takayama and Ando, 1934.
Uda, 1935a.
Eggs
Watanabe, H., 1939.
Enemies
Bennett, 1840.
Exploitation rates
Tauchi, 1940c.
Figured
Anonymous, 1938.
Barnhart, 1936.
Clemens and Wilby, 1946.
Cooper, 1863.
Fowler, 1904a.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Griffin, 1927.
Günther, 1876.
Holder, 1912.
Jordan and Evermann, 1905, 1926b.

Thunnus germo—Continued
Figured—Continued
Kishinouye, 1915a, 1923.
Kitahara, 1897.
Nakamura, 1949.
Roedel, 1948b.
Serventy, 1941.
Shapiro, 1948a.
Tinker, 1944.
Walford, 1931, 1937.
Fishing conditions correlated with area
Hart and Hollister, 1947.
Hart et al., 1948.
Fishing conditions correlated with oceanography
Aikawa, 1933.
Chiba Pref. Fish. Expt. Sta., Katsuura Br., 1936, 1941.
Hart and Hollister, 1947.
Hart et al., 1948.
Inanami, 1942d.
Japanese Bur. Fish., 1939, 1940.
Kagoshima Pref. Fish. Expt. Sta., 1927a, 1928b, 1930b, 1930c, 1931b, 1932b, 1932c, 1933b.
Kanamura and Yazaki, 1940b.
Kimura, 1942a, 1949.
Mie Pref. Fish. Expt. Sta., 1930c, 1930e.
Nakamura, 1949.
Sasaki, 1939b.
Scagel, 1949.
Shapiro, 1948a.
Takayama and Ando, 1934.
Uda, 1940c.
Uda and Tokunaga, 1937.
Fishing conditions correlated with season
Hart et al., 1948.
Fishing grounds correlated with oceanography
Soc. Prom. Ocean. Fish., 1936.
Food
Anonymous, 1938.
Asano, 1939.
Bennett, 1840.
Clemens and Wilby, 1946.
Hart and Hollister, 1947.
Hart et al., 1948.
Japanese Bur. Fish., 1939, 1940.
Jordan and Gilbert, 1881b, 1882.
Kanamura and Yazaki, 1940b.
Kishinouye, 1917b, 1923.
Kuronuma, 1940.
Nakamura, 1943, 1949.
Scagel, 1949.
Shapiro, 1948a.
Starks, 1918.
Starks and Morris, 1907.
Walford, 1937.
Watanabe, H., 1939.
Growth
Aikawa and Kato, 1938.
Brock, 1943.
Kishinouye, 1923.

Thunnus germo—Continued
Habits
Jordan and Gilbert, 1882.
Kishinouye, 1923.
Nakamura, 1949.
Shapiro, 1948a.
Hormones
Toyama et al., 1941.
Keys
Brock, 1949.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Jordan and Evermann, 1926b.
Kishinouye, 1915a, 1923.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Nakamura, 1949.
Okada and Matsubara, 1938.
Roedel, 1948b.
Serventy, 1941.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931, 1937.
Measurement data
Aikawa and Kato, 1938.
Anonymous, 1938.
Brock, 1943.
Godsil, 1948.
Godsil and Byers, 1944.
Ikebe, 1940c.
Japanese Bur. Fish., 1939, 1940.
Kanamura and Yazaki, 1940b.
Ōita Pref. Fish. Expt. Sta., 1925, 1927a.
South Seas Govt.- Gen. Fish. Expt. Sta., 1943a.
Uno, 1936b.
Watanabe, H. 1939.
Meristic characters
Clark, 1929.
Godsil and Byers, 1944.
Migration
Cobb, 1919.
Kimura, 1942b.
Kishinouye, 1923.
Kōchi Pref. Fish. Expt. Sta., 1923b, 1924.
Nakamura, 1943, 1949.
Sasaki, 1939b.
Shapiro, 1948a.
Soc. Prom. Ocean. Fish., 1936.
Walford, 1937.
Populations
Brock, 1943.
Clark, 1929.
Godsil, 1948, 1949.
Godsil and Byers, 1944.
Tauchi, 1940c.
Uda and Tokunaga, 1937.
Reproduction
Brock, 1943.
Nakamura, 1943.

Thunnus germo—Continued
Reproduction—Continued
Schaefer, 1948c.
Soc. Prom. Ocean. Fish., 1936.
Walford, 1937.
Watanabe, H., 1939.
Sex ratio
Brock, 1943.
Sexual maturity
Anonymous, 1938.
Clark, 1929.
Kanamura and Yazaki, 1940b.
Soc. Prom. Ocean. Fish., 1936.
Watanabe, H., 1939.
Size composition
Aikawa and Kato, 1938.
Brock, 1943.
Hart et al., 1948.
Kimura, 1942a.
Sasaki, 1939b.
Seagel, 1949.
Tauchi, 1940c.
Survival rates
Tauchi, 1940c.
Synonymy
Boeseman, 1947.
FAO, 1949.
Fish, 1948.
Fowler, 1904b, 1928.
Fraser-Brunner, 1950.
Griffin, 1927.
Günther, 1860, 1876.
Jordan and Evermann, 1896, 1905, 1926b.
Jordan and Gilbert, 1882.
Jordan and Hubbs, 1925.
Jordan, Tanaka, and Snyder, 1913.
Kishinouye, 1923.
McCulloch, 1922.
Meek and Hildebrand, 1923.
Nakamura, 1939b, 1949.
Phillipps, 1927b.
Schultz and DeLacy, 1936.
Soldatov and Lindberg, 1930.
Tanaka, 1931.
Ulrey and Greeley, 1928.
Tagging
Seagel, 1949.
Young
Kishinouye, 1917b, 1919b, 1923.
Lütken, 1880.
Schaefer, 1948c.
Thunnus maccori. See *Thunnus maccoyi*.
Thunnus maccoyi
Catch per unit of effort
Serventy, 1947.
Classification
Roughly, 1916.
Common names
Serventy, 1941.
Whitley, 1947.
Thunnus maccoyi—Continued
Compared with *Kishinoella tonggol*
Serventy, 1941.
Description
Castelnau, 1872.
Jordan and Evermann, 1926b.
Macleay, 1881.
Roughly, 1916.
Serventy, 1941.
Stead, 1908.
Distribution
Jordan and Evermann, 1926b.
Lord, 1927.
Macleay, 1881.
McCulloch, 1922.
Roughly, 1916.
Serventy, 1941, 1947.
Stead, 1908.
Waite, 1928.
Whitley, 1947.
Figured
McCulloch, 1922.
Roughly, 1916.
Serventy, 1941.
Habits
Roughly, 1916.
Keys
Jordan and Evermann, 1926b.
McCulloch, 1922.
Serventy, 1941.
Length-weight relation
Serventy, 1941.
Migration
Serventy, 1941.
Reproduction
Serventy, 1941.
Size composition
Serventy, 1941, 1947.
Synonymy
Jordan and Evermann, 1926b.
McCulloch, 1922.
Thunnus macropterus. See *Neothunnus macropterus*.
Thunnus maculatus
Distribution
Holder, 1912.
Figured
Holder, 1912.
Thunnus mebachi. See *Parathunnus mebachi*.
Thunnus nicolsoni
Compared with *Kishinoella tonggol*
Serventy, 1942b.
Thunnus obesus. See also *Parathunnus mebachi* and *Parathunnus sibi*.
Classification
Fraser-Brunner, 1950.
Description
Fraser-Brunner, 1950.
Distribution
Fraser-Brunner, 1950.

Thunnus obesus—Continued
Figured
Fraser-Brunner, 1950.
Keys
Fraser-Brunner, 1950.
Synonymy
Fraser-Brunner, 1950.
Thunnus orientalis
Age
Aikawa and Kato, 1938.
Kimura, 1935.
Tauchi, 1940a.
Anatomy
Kishinouye, 1915a, 1915b, 1919a, 1921, 1922a, 1923.
Migita and Arakawa, 1948.
Nakamura, 1938, 1949.
Suyehiro, 1942.
Body condition
Aikawa and Kato, 1938.
Body temperature
Ōita Pref. Fish. Expt. Sta., 1927a, 1930.
Chemical analysis
Miyama and Osakabe, 1938, 1940.
Miyauchi, 1915.
Shimizu, 1947.
Classification
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Shapiro, 1948a.
Common names
Fujita and Wakiya, 1915.
Jordan and Hubbs, 1925.
Jordan and Snyder, 1901.
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Shapiro, 1948a, 1948b.
Tinker, 1944.
Compared with *Thunnus thynnus*
Kishinouye, 1921.
Soc. Prom. Ocean. Fish., 1936.
Tinker, 1944.
Description
Boeseman, 19
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1949.
Okada and Matsubara, 1938.
Shapiro, 1948a.
Temminck and Schlegel, 1850.
Tinker, 1944.
Distribution
Fowler, 1934.
Fujita and Wakiya, 1915.
Jordan and Evermann, 1926a, 1926b.
Jordan and Hubbs, 1925.
Jordan and Jordan, 1922.
Thunnus orientalis—Continued
Distribution—Continued
Jordan and Snyder, 1900, 1901.
Kimura, 1942b.
Kishinouye, 1915a, 1923.
Kōchi Pref. Fish. Expt. Sta., 1924.
Matsubara, 1943.
Mori, 1928.
Nakamura, 1938, 1939b, 1943, 1949.
Okada and Matsubara, 1938.
Reeves, 1928.
Richardson, 1846.
Shapiro, 1948a, 1948b.
Tinker, 1944.
Distribution correlated with water temperature
Takayama and Ando, 1934.
Eggs
Hatai et al., 1941.
Nakamura, 1938, 1949.
Enemies
Kishinouye, 1923.
Exploitation rates
Tauchi, 1940a.
Figured
Kishinouye, 1915a, 1923.
Nakamura, 1939b, 1949.
Otaki, Fujita, and Higurashi, 1903.
Shapiro, 1948a.
Tinker, 1944.
Fishing conditions correlated with astronomical phenomena
Kawana, 1934.
Fishing conditions correlated with oceanography
Aikawa, 1933.
Fukuda and Iizuka, 1940a.
Iehisa, 1939.
Kagoshima Pref. Fish. Expt. Sta., 1927a, 1930c, 1932b.
Kawana, 1934, 1937.
Mie Pref. Fish. Expt. Sta., 1930c, 1930e.
Ōita Pref. Fish. Expt. Sta., 1930.
Okinawa Pref. Fish. Expt. Sta., 1940b.
Ōmori and Fujimoto, 1940.
Ōmori and Fukuda, 1938, 1940.
Shapiro, 1948a.
Takayama and Ando, 1934.
Uda, 1940c.
Fishing conditions correlated with weather
Ōita Pref. Fish. Expt Sta., 1930.
Food
Kishinouye, 1923.
Nakamura, 1943, 1949.
Shapiro, 1948a.
Suyehiro, 1942.
Growth
Aikawa and Kato, 1938.
Kimura, 1932.
Kishinouye, 1923.
Habits
Kishinouye, 1923.
Nakamura, 1949.
Shapiro, 1948a.

Thunnus orientalis—Continued
Hormones
Migita and Arakawa, 1948.
Keys
Brock, 1949.
Jordan and Evermann, 1926b.
Kishinouye, 1915a, 1923.
Nakamura, 1949.
Okada and Matsubara, 1938.
Measurement data
Aikawa and Kato, 1938.
Higashi, 1940a.
Ōita Pref. Fish. Expt. Sta., 1927a, 1930.
Migration
Kimura, 1942b.
Kishinouye, 1923.
Kōchi Pref. Fish. Expt. Sta., 1924.
Nakamura, 1943, 1949.
Shapiro, 1948a.
Populations
Tauchi, 1940a.
Reproduction
Hatai et al., 1941.
Kishinouye, 1915a, 1923.
Nakamura, 1938, 1939b, 1943, 1949.
Soc. Prom. Ocean. Fish., 1936.
Sexual maturity
Hatai et al., 1941.
Nakamura, 1938.
Size composition
Aikawa and Kato, 1938.
Kawana, 1934.
Kimura, 1932, 1935.
Mine and Iehisa, 1940.
Tauchi, 1940a.
Survival rates
Tauchi, 1940a.
Synonymy
Boeseman, 1947.
Fowler, 1934.
Jordan and Evermann, 1926b.
Jordan and Hubbs, 1925.
Kishinouye, 1923.
Nakamura, 1939b, 1949.
Richardson, 1846.
Tagging
Kawana, 1934.
Young
Kishinouye, 1919b, 1923.
Thunnus phillippsi
Classification
Phillipps, 1927b.
Common names
Phillipps, 1927b.
Description
Jordan and Evermann, 1926b.
Distribution
Jordan and Evermann, 1926b.
Phillipps, 1927b.
Figured
Jordan and Evermann, 1926b.
Thunnus orientalis—Continued
Keys
Jordan and Evermann, 1926b.
Synonymy
Phillipps, 1927b.
Thunnus phillipsi. See *Thunnus phillippsi*.
Thunnus rarus. See *Neothunnus rarus*.
Thunnus salicus
Common names
Craig, 1929.
Description
Jordan and Evermann, 1926b.
Distribution
Jordan and Evermann, 1926b.
Ulrey, 1929.
Figured
Jordan and Evermann, 1926b.
Keys
Jordan and Evermann, 1926b.
Thunnus schlegeli. See *Thunnus orientalis*.
Thunnus thunnina. See *Euthynnus alletteratus*.
Thunnus thunnus. See *Thunnus thynnus*.
Thunnus thynnus
Anatomy
Fish, 1948.
Godsil and Byers, 1944.
Kishinouye, 1921.
Catch per unit of effort
Whitehead, 1931.
Chemical analysis
Dill, 1921.
Classification
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Roedel, 1948b.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931.
Whitehead, 1931.
Common names
Barnhart, 1936.
FAO, 1949.
Fish, 1948.
Jordan and Evermann, 1896.
Jordan, Tanaka, and Snyder, 1913.
Roedel, 1948b.
Schultz, 1949.
Starks and Morris, 1907.
Tinker, 1944.
Ulrey and Greeley, 1928.
Walford, 1931, 1937.
Compared with *Neothunnus macropterus*
Thompson and Higgins, 1919.
Compared with *Thunnus orientalis*
Kishinouye, 1921.
Soc. Prom. Ocean. Fish., 1936.
Tinker, 1944.
Description
Barnhart, 1936.
Fowler, 1928, 1944.
Fraser-Brunner, 1950.

Thunnus thynnus—Continued
Description—Continued
Godsil and Byers, 1944.
Günther, 1876.
Meek and Hildebrand, 1923.
Roedel, 1948b.
Soldatov and Lindberg, 1930.
Starks, 1918.
Stead, 1906.
Tinker, 1944.
Walford, 1931, 1937.
Distribution
Abe, 1939.
Barnhart, 1936.
Brock, 1938.
FAO, 1949.
Fish, 1948.
Fowler, 1923a, 1923b, 1928, 1929, 1931, 1934, 1938, 1944.
Fraser-Brunner, 1950.
Gilbert and Starks, 1904.
Günther, 1876.
Herre, 1936, 1940.
Hildebrand, 1946.
Holder, 1912.
Jordan and Evermann, 1896.
Jordan and Jordan, 1922.
Jordan, Tanaka, and Snyder, 1913.
Meek and Hildebrand, 1923.
Metz, 1912.
Roedel, 1948b.
Schultz, 1949.
Schultz and DeLacey, 1936.
Soldatov, 1929.
Soldatov and Lindberg, 1930.
Starks, 1918.
Starks and Morris, 1907.
Stead, 1906.
Tanaka, 1931.
Taranetz, 1937.
Tinker, 1944.
Ulrey, 1929.
Ulrey and Greeley, 1928.
Waite, 1921.
Walford, 1931, 1937.
Whitehead, 1929, 1931.
Distribution correlated with water temperature
Uda, 1935a.
Enemies
Tinker, 1944.
Walford, 1937.
Figured
Barnhart, 1936.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Holder, 1912.
Kitahara, 1897.
Roedel, 1948b.
Soldatov and Lindberg, 1930.
Starks, 1918.
Tinker, 1944.
Thunnus thynnus—Continued
Figured—Continued
Walford, 1931, 1937.
Whitehead, 1931.
Fishing conditions correlated with oceanography
Kida, 1936.
Food
Tinker, 1944.
Walford, 1937.
Habits
Kida, 1936.
Uchida, 1923.
Keys
Brock, 1949.
Fraser-Brunner, 1950.
Godsil and Byers, 1944.
Hildebrand, 1946.
Meek and Hildebrand, 1923.
Roedel, 1948b.
Soldatov and Lindberg, 1930.
Taranetz, 1937.
Walford, 1931, 1937.
Measurement data
Godsil and Byers, 1944.
Uda, 1932.
Meristic characters
Godsil and Byers, 1944.
Migration
Whitehead, 1931.
Populations
Godsil and Byers, 1944.
Reproduction
Tinker, 1944.
Walford, 1937.
Whitehead, 1931.
Size composition
Kida, 1936.
Synonymy
FAO, 1949.
Fish, 1948.
Fowler, 1928, 1934, 1944.
Fraser-Brunner, 1950.
Günther, 1876.
Herre, 1936.
Jordan and Evermann, 1896.
Jordan, Tanaka, and Snyder, 1913.
Meek and Hildebrand, 1923.
Schultz, 1949.
Schultz and DeLacy, 1936.
Soldatov and Lindberg, 1930.
Tanaka, 1931.
Ulrey and Greeley, 1928.
Waite, 1921.
Thunnus tonggol
Classification
Fraser-Brunner, 1950.
Compared with *Kishinoella tonggol*
Serventy, 1942b.
Description
Bleeker, 1852.

Thunnus tonggol—Continued
Description—Continued
Fraser-Brunner, 1950.
Günther, 1860.
Distribution
Bleeker, 1852, 1861b.
Fraser-Brunner, 1950.
Günther, 1860.
Figured
Fraser-Brunner, 1950.
Serventy, 1942b.
Keys
Fraser-Brunner, 1950.
Synonymy
Bleeker, 1852.
Fraser-Brunner, 1950.
Günther, 1860.
Thunnus zacalles. See *Kishinoella zacalles*.
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Temperature—Continued
Correlated with fishing conditions—Continued
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Correlated with fishing
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BREEDING HABITS OF LAKE TROUT IN NEW YORK

By WILLIAM F. ROYCE

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CONTENTS

	Page
Sexual dimorphism	59
Spawning habits	61
Age and size at maturity	61
Time of spawning	62
Duration of spawning period	65
Place of spawning	66
Spawning act	68
Environment and development of eggs and larvae	70
Efficiency of fertilization	70
Temperature requirements	71
Effects of predation	71
Development of eggs and alevins	72
Juvenile lake trout of Keuka Lake	73
Summary	74
Acknowledgments	75
Literature cited	75

BREEDING HABITS OF LAKE TROUT IN NEW YORK

By WILLIAM F. ROYCE, *Fishery Research Biologist*

The several races of lake trout (*Salvelinus* [=*Cristivomer*] *namaycush*) are widely sought in all the more accessible parts of their range. In the Great Lakes, where this species is one of the most valued food fishes, it is the object of a major fishery. In smaller lakes of the northeastern United States and southern Canada, where commercial fishing usually is prohibited, it is sought as a game fish.

This popularity has been accompanied by severe declines in the populations of lake trout in some lakes, notably the Great Lakes. Detailed knowledge of the species, particularly of the eggs, larvae, and juveniles below the sizes commonly caught, is needed for devising measures to prevent such declines, and for successfully introducing this desirable species in additional lakes.

Almost nothing is known of the habits of young lake trout, probably because of their deep-water habitat; in fact, very few wild lake trout less than 8 inches long have even been seen. The reproductive habits of the species have been imperfectly known, and very little has been published on size and age at maturity. Accordingly, a study of the breeding habits of this species and the life history of its young was made in 1939, 1940, and 1941, on several lakes in the State of New York.

SEXUAL DIMORPHISM

The lake trout, unique among the salmon family, lacks almost completely the malformed jaws or kype common to mature males of other species. Examination of several hundred lake trout from various lakes in New York State showed that it is almost impossible to distinguish the sex of mature lake trout by examination of the head alone. The males have only a slight tendency toward a more pointed snout—although J. R. Westman reported in a personal communication that he had seen a very large male lake trout from Lake Simcoe, Ontario, with a well-developed kype.

It is pertinent to compare the jaws of the lake trout with those of the Pacific salmon, in which the kype attains its maximum development. The Pacific salmon migrate enormous distances to the spawning ground and live entirely on stored food for almost a year before spawning. Mottley (1936) [1] suggests that the development of the kype in the male may occur because its demand on the material mobilized for the development of the gonads differs from that of the female. He postulates that the ovaries would have a general requirement for stored materials, while the testes would require little albuminoid or fat. Thus, these materials might be utilized in the growth of the kype instead of being excreted.

The lake trout would appear to be a diametric opposite. It rarely has a kype, migrates only the short distance from the deep to the shoal waters of a lake, and feeds up to and through the spawning period.[2] Inasmuch as the lake trout does not acquire a kype and as the maturation of the gonads parallels that of the salmon, Mottley's suggestion leaves some things to be explained. Possibly, since the lake trout feeds right up to and through the spawning season, the gonads can develop from ingested food instead of mobilizing stored material from the body.

Alike in external structure, male and female lake trout are also very similar in color when removed from the water. However, in New York State, the normal coloration of both sexes varies widely from lake to lake. The lake trout of the large, clear Finger Lakes are light olivaceous, almost silvery on the back and sides, with a little yellow or orange in the fins. There are all gradations between the color of these trout and the very dark trout of the brown-water Adirondack lakes.

NOTE.—This paper is a revision of a thesis that was submitted to Cornell University in 1943 in partial fulfillment of the requirements for the degree of doctor of philosophy.

[1] Publications referred to parenthetically by date are listed in Literature Cited, p. 75.

[2] Rayner (1941) found that stomachs of ripe lake trout taken on the spawning area contained fish, lake-trout eggs, and miscellaneous invertebrates.

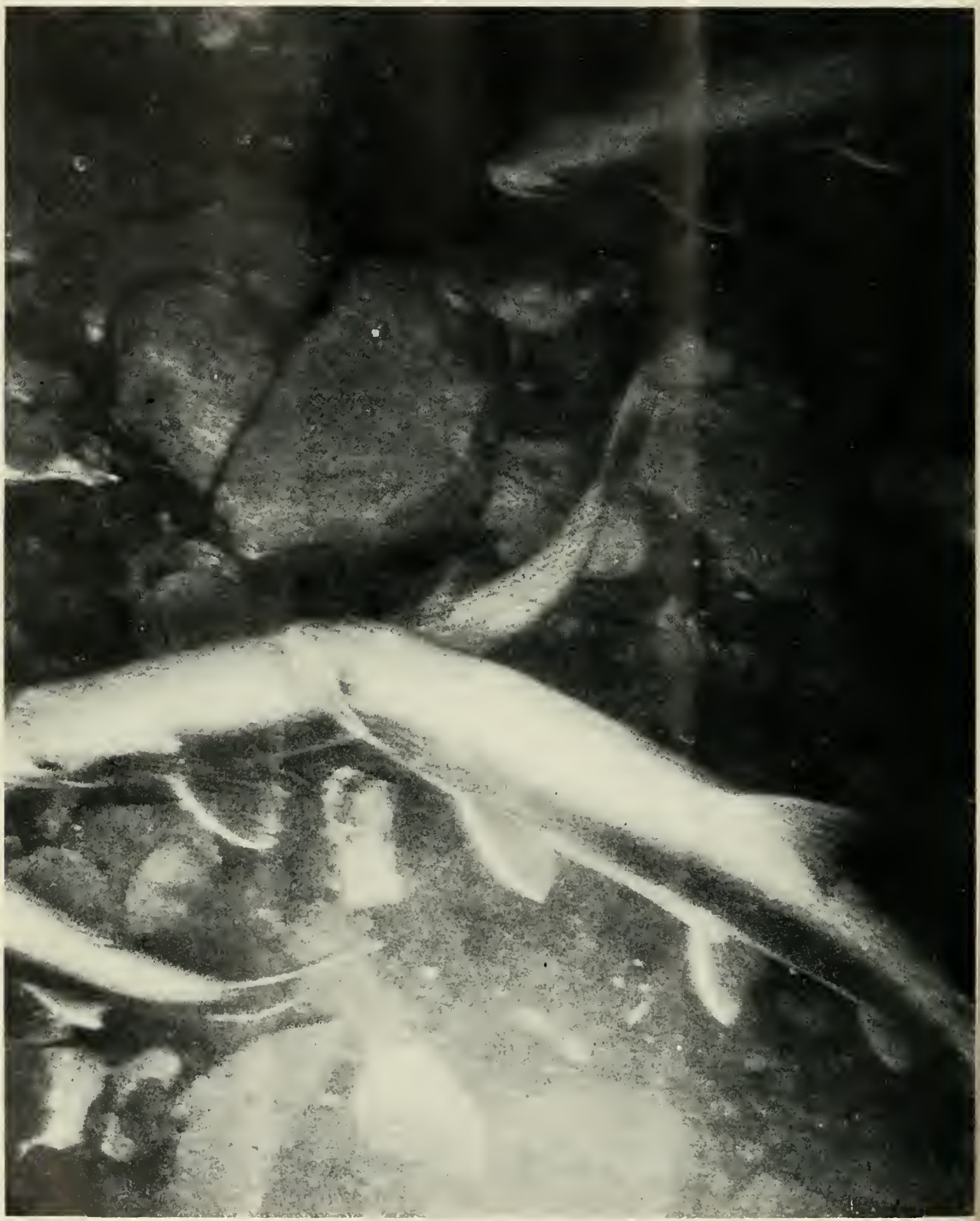

FIGURE 1.—Male lake trout on the spawning grounds in Otsego Lake, N. Y.

The latter have stronger colors, and the sexual differences are a little more pronounced; the males tend to have more brilliant yellow, orange, and black in the paired fins than the females. But even in these lake trout it is not always possible to distinguish the sexes on the basis of external differences.

This normal coloration is considerably changed when the male lake trout are excited on the spawning area. While they are courting, the chromatophores on their backs contract, making the backs appear decidedly light colored, while the sides, flooded with pigment, become very lustrous and almost black (fig. 1). Merriman (1935) observed this condition in the lake trout of Squam Lake, N. H., and it was seen by the writer in Otsego Lake, N. Y., in 1940 and 1941, when selected fish were speared and the brilliant coloration was found to be restricted to the males. Striking as this coloration was during the courting or spawning, the colors were most ephemeral. After the fish were netted or speared, color differences between the sexes could not be detected.

SPAWNING HABITS

AGE AND SIZE AT MATURITY

The age analysis, by means of scales, of 33 mature lake trout caught by gill net on the spawning area off Peach Orchard Point in Seneca Lake, N. Y., showed that 13 had 5 annuli and the remaining 20 had 6 annuli. Comparison of the lengths of the lake trout in this sample with the length frequency of 424 lake trout taken during the spawning season in 1941 showed that these age groups comprised the bulk of the catch, but probably an appreciable quantity of older fish were taken.

Data collected during 1940 by J. R. Westman on the lake trout of Lake Simcoe, Ontario, showed that 13 out of 20 five-year-old and 16 out of 17 six-year-old lake trout were mature. Samples from Keuka Lake, N. Y., in the same year showed similar results: 15 out of 18 five-year-old and 5 out of 6 six-year-old trout were mature. There was a slight tendency for the greater proportion of the young males to be mature in these two lakes, as well as in Seneca Lake.

Fry and Kennedy (1937) estimated, by means of the modes of a length frequency distribution, that the lake trout of Lake Opeongo, Algonquin Park, Canada, reached the minimum age at maturity in their fifth year of life (corresponding, presumably, to four annuli). Inasmuch as they had only five lake trout less than 13 inches long, and as my observations indicate very small growth of lake trout in the first year, I believe that they assigned to each mode an age 1 year less than it should have been.

These data are substantiated by studies made on the growth of hatchery-reared trout. Surber (1933) secured eggs from female lake trout, aged 4 years 6 months, whose lengths varied from 18 to 26 inches; but at this time only 10 females out of somewhat less than 2,000 males and females spawned, producing an average of only 962 eggs per female. No data on subsequent spawning were presented, but certainly the majority of these fish did not spawn before their sixth year. Surber considered that this age at maturity was comparable to that attained by wild fish. He gave the length of the trout at the end of their first, second, third, and fourth years of life as 10, 14, 16 to 18, and 18 to 26 inches, respectively. This rate of growth in the first and second years of life is markedly greater than that existing in Keuka Lake. With this start it is possible that the hatchery fish spawned earlier than they would in the wild, which is known to be true of some other species of hatchery-reared trout, especially brook trout.

The rapidly growing lake trout of Seneca Lake, whatever their age, do not mature until they are 26 to 30 inches in total length; those of Keuka Lake mature at a total length of 18 to 24 inches. In Skaneateles Lake, N. Y., however, Rayner (1941) captured many mature lake trout of 15 and 16 inches total length. Fry (1939) reported that the minimum size at maturity in some lakes of Algonquin Park, Canada, varied from 14 to 18 inches according to the lake.

Obviously with this variation in size at maturity, a uniform minimum legal-size limit of 15 inches, such as exists in New York State, may permit the taking of many immature, rapidly growing fish in some lakes while providing entirely too much protection in other lakes. It would appear necessary to consider the growth rate and fishing pressure in each lake in setting a minimum size limit.

Slowly growing lake trout may be subject to senility at a small size. Fry and Kennedy (1937) reported that none of the lake trout of more than

22 inches fork length in Lake Opeongo, Algonquin Park, Ontario, were capable of spawning. Such widespread impotency was not observed in any of the New York lake trout. The conservation department employees engaged in spawn-taking operations on the Adirondack and Finger Lakes reported that only occasionally would an impotent fish be found. The more limited observations I made also failed to show any impotency, and it is quite likely that after the lake trout in New York State lakes are mature they may spawn several times before succumbing to the infirmities of age.

TIME OF SPAWNING

The available information shows that lake trout, and most other trout, spawn once a year in the fall when the temperature is dropping and the days are becoming shorter. Among different races of lake trout, small variations in the spawning date are found. This is true also of the same race of lake trout in different lakes, and of the same race in the same lake in different years. It appears probable that fluctuations in light and temperature, in the physical characteristics of different lakes, and in the responses of different races are the determining factors.

These factors have proved important in influencing the spawning time of other species. Hoover and Hubbard (1937) have shown that brook trout which normally spawned in December could be induced to spawn in late August and early September by increasing the amount of light in early spring and decreasing it in late summer. Bissonette and Burger (1940) state that "there is no uniform control of the sexual cycle applicable to all fish. In some fish, temperature seems to be the major factor; in others, light and temperature play cooperative roles; while in still others, light appears to be the most important factor."

Merriman and Schedl (1941), on the basis of laboratory experiments on the four-spined stickleback, *Apeltes quadracus* (Mitchill), concluded that light influenced oögenesis but not spermatogenesis, while temperature somewhat unequally affected the maturation of the gonads of both sexes. McCay et al. (1930) concluded on the basis of feeding experiments that the spawning time of brook trout could be influenced by the food supply. They found that the age at maturity could be advanced or postponed by increasing or decreasing the amount of food fed to the hatchery trout, but the question of changing the spawning date of mature trout was not clarified.

After several years of netting lake trout in Raquette Lake for spawn taking, the hatchery men of the New York Conservation Department have observed that the lake trout run earlier after a sudden drop in temperature. The extensive data on their operations were made available to me, and weather data were obtained from the United States Weather Bureau (table 1).

TABLE 1.—*Weather conditions in relation to peak of lake-trout egg take at Raquette Lake, 1933–41*

Year	Air temperature [1] (° F.)	Cloudy days [2]	Peak of egg take
1933	56.8	22	Oct. 22
1934	54.9	21	Oct. 18
1935	52.4	24	Oct. 13
1936	54.0	19	Oct. 19
1937	55.0	21	Oct. 21
1938	[3]	[3]	[3]
1939	55.4	18	Oct. 23
1940	53.4	22	Oct. 19
1941	56.6	21	Oct. 19

[1] Average air temperature for the month of September at nearby Indian Lake.
[2] Number of cloudy days in July, August, and September in the northern plateau region of New York.
[3] No eggs taken.

The average air temperature for September reported by the Indian Lake weather station was used because it was the nearest station to Raquette Lake, with complete weather records for the 8 years of spawning data. The average number of cloudy days for the entire northern plateau region of New York was selected because many of the smaller stations had no automatic sunshine recorders and their estimates of cloudiness varied considerably. The number of cloudy days in July, August, and September was used because the work of Hoover and Hubbard (1937) indicated that changes in the light required a considerable time to influence the development of the eggs, and these 3 months were the ones preceding the spawning season which had decreasing amounts of daylight.

The analysis of these data by multiple regression (table 2) indicated that the date of spawning was advanced by lower temperatures or a greater number of cloudy days and retarded by warmer weather or fewer cloudy days. However, neither on air temperature alone nor on cloudiness alone

was the partial regression of the spawning date statistically significant. When both factors were considered in a multiple regression coefficient the result was significant (R=.8643 when R of .836 or greater is to be expected 5 percent of the time with 5 degrees of freedom).

TABLE 2.—*Reduced data for multiple regression analysis of the date of peak of lake-trout egg take at Raquette Lake*

x_1=Average air temperature for the month of September at Indian Lake.

x_2=Number of cloudy days in July, August, and September in the northern plateau region of New York.

y=Date of peak of lake-trout egg take.

Number of observations: $n=8$

Means:

$$\bar{x}_1=54.81 \qquad \bar{x}_2=21.00 \qquad \bar{y}=19.25$$

Sums of squares:

$$Sx_1^2=16.01 \qquad Sx_2^2=24.00 \qquad Sy^2=65.50$$

Sums of products:

$$Sx_1x_2=-6.80 \qquad Sx_2y=-27.00 \qquad Sx_1y=23.08$$

Correlation coefficients:

$$r_{12}=-.3469 \qquad r_{y2}=-.6810 \qquad r_{y1}=.7534$$

Standard partial regression coefficients:

$$B_{y1.2}=.5675 \qquad B_{y2.1}=-.4841$$

Multiple regression equation:

$$E=-80.3+2.32X_1-1.32X_2$$

TESTS OF SIGNIFICANCE:

Standard partial regression coefficients: ($DF=5$)

$$\text{for } B_{y1.2}\ t=\frac{.5675}{.2398}=2.366$$

$$\text{for } B_{y2.1}\ t=\frac{.4841}{.2398}=2.019$$

neither significant

Multiple correlation or multiple regression: ($DF=5$)

R=.8643 significant

A similar analysis of data on the peak of egg take from Upper Saranac Lake (tables 3 and 4) was less conclusive. The date of peak of egg take in 1941 was about a month later than usual, but if we omit this aberrant observation the date of the peak at Upper Saranac Lake seems to bear the same relation to air temperature and cloudiness as at Raquette Lake. However, neither the partial nor the multiple regression coefficients are significant. (R=.699 when R of .930 or greater is to be expected 5 percent of the time with 3 degrees of freedom).

TABLE 3.—*Weather conditions in relation to peak of lake-trout egg take in Upper Saranac Lake, 1935–41*

Year	Air temperature[1] (°F.)	Cloudy days[2]	Peak of egg take
1935	52.3	24	Oct. 17
1936	56.9	19	Oct. 23
1937	54.8	21	Oct. 21
1938	52.0	28	Oct. 15
1939	54.8	18	Oct. 24
1940	52.4	22	Oct. 26
1941	57.2	21	Nov. 20

[1] Average air temperature for the month of September at nearby Tupper Lake.
[2] Number of cloudy days in July, August, and September in the northern plateau region of New York.

TABLE 4.—*Reduced data for the multiple regression anaylsis of the date of the peak of lake-trout egg take at Upper Saranac Lake*

x_1=Average air temperature for the month of September at Tupper Lake.

x_2=Number of cloudy days in July, August, and September in the northern plateau region of New York.

y=Date of peak of lake-trout egg take.

Number of observations: $n=6$ [1]

Means:

$$\bar{x}_1=53.87 \qquad \bar{x}_2=22.00 \qquad \bar{y}=21.00$$

Sums of squares:

$$Sx_1^2=19.03 \qquad Sx_2^2=66.00 \qquad Sy^2=90.00$$

Sums of products:

$$Sx_1x_2=-28.10 \qquad Sx_2y=-62.00 \qquad Sx_1y=19.00$$

Correlation coefficients:

$$r_{12}=-.7929 \qquad r_{y2}=-.6263 \qquad r_{y1}=.4591$$

Standard partial regression coefficients:

$$B_{y1.2}=-.1008 \qquad B_{y2.1}=-.7062$$

Multiple regression equation:

$$E=50.94-.219X_1-.825X_2$$

TESTS OF SIGNIFICANCE:

Standard partial regression coefficients: ($DF=3$)

$$\text{for } B_{y1.2}\ t=\frac{.1008}{.6776}=.1488$$

$$\text{for } B_{y2.1}\ t=\frac{.7062}{.6776}=1.0421$$

neither significant

Multiple correlation or multiple regression: ($DF=3$)

R=.6990 not significant

[1] 1941 data omitted.

Other things must be considered in evaluating these analyses. The data are few, only 6 years in one instance and 8 in the other, and the Weather Bureau data on air temperature and cloudiness cannot be a precise measurement of the temperature and the light actually affecting the fish. Furthermore, the period during which the light and the temperature changes are influential can only be surmised, and other factors may be important. For example, in Raquette Lake in 1938 the notably high water level was suspected of being the cause of almost no lake trout being caught. However, it was not certain whether this affected the migrations or prevented the nets from operating effectively.

Considering that a significant relation was established in one instance, and that other data were inconclusive but showed a similar tendency, it is probable that both light and temperature do influence the spawning time of lake trout.

Lake trout in Raquette Lake (Oliver R. Kingsbury, report to the New York Conservation Department, November 1935) spawn at about the time of the lake turn-over. In the middle of the 1935 spawning season, temperatures taken at the surface and at depths down to 56 feet revealed no more than a 3° F. difference between top and bottom. This seems to be more important than the actual surface temperature in influencing spawning, for the surface temperature on the day the first eggs were taken was 58° F. in 1933, 52° F. in 1934, and 50° F. in 1935. Merriman (1935) reports lake trout spawning in Squam Lake, N. H., when the surface temperature was 42° F. In Otsego Lake in 1940 the lake trout were observed spawning December 5, when the surface temperature was 37° F. No facilities were available for taking deep-water temperatures at that time, but in 1941 the fish were observed late in their spawning season on December 3, when the water temperature was uniformly 43° F. from the surface down to 60 feet. These wide variations in surface temperature indicate its slight value as a determinant of the date of spawning.

Such differences in the progress of cooling in different lakes are probably associated with the depths of the lakes, and it appears that the depth of a lake is associated with the time of lake-trout spawning. Table 5 presents data from the files of the New York State Conservation Department on the time and duration of lake-trout spawn taking operations in some New York lakes. Figure 2, which incorporates information from table 5, from Rayner (1941) for Skaneateles Lake, and from my observations on Otsego Lake, shows this relation graphically.

TABLE 5.—*Duration of lake-trout spawn taking operations by State Conservation Department in some New York lakes*

Year	Date first eggs received at hatchery	Date of peak of egg take	Date last eggs received at hatchery
Raquette Lake (alt. 1,762 ft.; max. depth 96 ft.):			
1933	Oct. 14	Oct. 22	Oct. 24
1934	Oct. 14	Oct. 18	Oct. 20
1935	Oct. 11	Oct. 13	Oct. 16
1936	Oct. 16	Oct. 19	Oct. 21
1937	Oct. 16	Oct. 21	Oct. 26
1939	Oct. 16	Oct. 23	Oct. 26
1940	Oct. 12	Oct. 19	Oct. 24
1941	[1]	Oct. 19	[1]
Lake George (alt. 322 ft.; max. depth 187 ft.):			
1928	Nov. 5	[1]	Nov. 14
1929	Oct. 31	[1]	Nov. 5
1932	Nov. 5	[1]	Nov. 13
1936	Nov. 2	Nov. 6	Nov. 9
1938	Nov. 4	Nov. 8	Nov. 11
Lake Pleasant (alt. 1,724 ft.; max. depth 53 ft.):			
1930	[1]	Oct. 14	[1]
1932	Oct. 12	[1]	Oct. 15
Sacandaga Lake (alt. 1,724 ft.; max. depth 60 ft.):			
1929	Oct. 13	[1]	Oct. 13
1930	[1]	Oct. 22	Oct. 26
1932	Oct. 12	Oct. 16	Oct. 23
1933	Oct. 16	Oct. 21	Oct. 23
Piseco Lake (alt. 1,661 ft.; max. depth 129 ft.):			
1930	Oct. 17	Oct. 25	Oct. 29
1931	Oct. 15	Oct. 24	Nov. 5
1932	Oct. 13	[1]	Oct. 28
1933	Oct. 10	[1]	Oct. 15
Seventh Lake (alt. 1,786 ft.; max. depth 85 ft.):			
1933	Oct. 20	Oct. 24	Oct. 24
Seneca Lake, (alt. 444 ft.; max. depth 625 ft.):			
1939–41 [2]	Sept. 23	Oct. 10	Nov. 3
Keuka Lake (alt. 709 ft.; max. depth 187 ft.):			
1936–39 [2]	Nov. 20	Nov. 25	Dec. 3
Upper Saranac Lake (alt. 1,571 ft.; max. depth 100 ft.):			
1935	[3]	Oct. 17	[3]
1936	[3]	Oct. 23	[3]
1937	[3]	Oct. 21	[3]
1938	[3]	Oct. 15	[3]
1939	[3]	Oct. 24	[3]
1940	[3]	Oct. 26	[3]
1941	[3]	Nov. 20	[3]

[1] Data not available.
[2] Same dates were reported for each year.
[3] Data depended on hatchery schedule rather than lake-trout migrations.

It appears that the lake trout spawn early in the shoal lakes and later in the deep lakes. If, as indicated previously, they spawn at about the turn-over time of the lake, this would be expected, as the deeper lakes cool off more slowly.

Like so many rules, the one that the deeper the lake the later the lake trout spawn has an outstanding exception. In Seneca Lake, the deepest lake in New York State (625 feet maximum depth), the lake trout spawn the earliest. They start in late September and continue through October, spawning in water from 100 to 200 feet

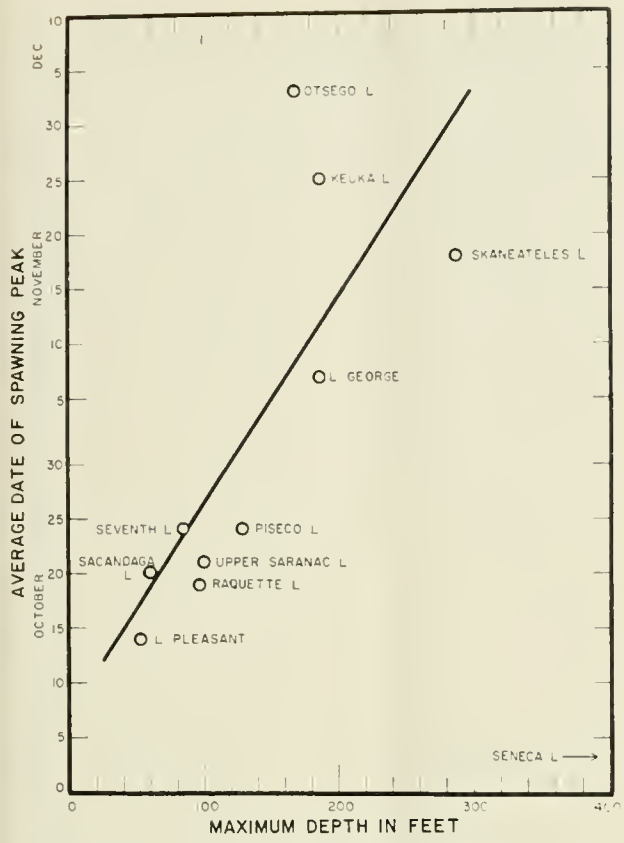

FIGURE 2.—Relation of average date of peak of lake-trout spawning activity and maximum depth of some New York lakes.

deep at a time well in advance of the turn-over period of the lake. Data taken from September 29 to October 17, 1941, showed that the surface temperature ranged from 57° to 62° F.

This large deviation in the time of spawning may be attributed to racial differences in the lake trout. Milner (1874) gives the spawning time of the siscowet (*Cristivomer namaycush siscowet*) as late August and early September in the deep waters of Lake Superior. In the same lake the common lake trout (*Salvelinus* [=*Cristivomer*] *namaycush*) spawns in from 7 feet to 15 fathoms of water during the month of October and in early November (Milner 1874, Van Oosten 1935). Hubbs (1930) has described the Rush Lake trout (*Cristivomer namaycush huronicus*) and states that it spawns in deep water in late summer rather than in fall, as does the common lake trout in the same lake. Dymond (1926) gives the time of spawning of the common lake trout as the month of October in Lake Nipigon, Ontario. But he points out that there is a race of black trout in the same lake which ascends some of the tributary streams and starts spawning about September 20, and a third race which is said to spawn in deep water from October 20 to November 10.

In New York State the spawning data indicate that two races [3] of lake trout exist: One, the Seneca Lake trout, spawns early in deep water, and the other, widespread in the Finger and Adirondack Lakes, spawns in shallow water at about the time of the turn-over of the lake.

With these differences in reactions and spawning habits, it would be desirable to determine if the Seneca Lake trout can adapt themselves to the conditions existing in Adirondack Lakes and vice versa before extensive stocking is attempted. Until such knowledge can be secured it would be wise to stock lake trout in lakes similar to those from which the eggs were obtained.

DURATION OF THE SPAWNING PERIOD

Data on the receipt of lake-trout eggs at some of the New York State hatcheries are summarized in table 5. The date of receipt of eggs corresponds closely to the date of take, except for the first one or two days of the spawning season. Ordinarily, only a few ripe fish are found at first, and if only a few thousand eggs were obtained, they often were held for a day or two until more eggs were available to make the trip to the hatchery worth while. The date the first eggs were taken probably averages about 1 day earlier than the date of their receipt at the hatchery. At the peak of the spawning season the eggs were usually rushed to the hatchery immediately, so the date of the peak receipt of eggs corresponds to the date of the peak egg take.

The data in table 5 do not indicate the complete spawning season but rather the season during which it was feasible to catch and strip the trout. High water sometimes so affected the fishing of the nets that it was not practical to continue fishing, and bad weather sometimes cut short the stripping operations. Hence, a short period of egg take is not necessarily indicative of a

[3] Other evidence of racial difference is available. New York State fish hatchery foremen agreed that eggs from Seneca Lake trout averaged about 240 an ounce, while eggs of lake trout of comparable size from Adirondack lakes averaged about 200 to 210 an ounce. No measurements of the actual diameters of the eggs were available, but the counts of the hatchery foremen appeared to be fairly consistent. D. C. Haskell (unpublished material gathered in 1941) also reports that the Seneca Lake trout grow significantly faster under hatchery conditions than the young lake trout from Raquette and Upper Saranac Lakes.

short spawning season. It seems likely, however, that the longer periods of spawn taking closely approximate the spawning season.

It appears that the lake-trout spawning season lasts from 10 to 20 days in the smaller New York lakes and the duration is fairly uniform in the same lake from year to year. The lake trout of Lake George consistently completed their spawning in 7 to 10 days at the most.

The length of the spawning season increases in the larger lakes. Van Oosten (1935) gives the duration of the spawning season in Lake Michigan as October 10 to November 21; in Lake Huron, October 10 to November 15; and in Lake Superior, October 1 to November 6. Seneca Lake is similar to the Great Lakes in both date and duration of the spawning season. The earliest and latest dates on which the New York State Conservation Department obtained eggs in Seneca Lake were September 23 and November 3. These dates are for different years, but the earliest and latest dates were similar from year to year.

PLACE OF SPAWNING

The observations of Merriman (1935), Royce (1936), and the writer indicate that lake-trout spawning areas are restricted to bottom of clean gravel or rubble, free of sand and mud. As the fish make no effort to bury the eggs, the bottom must have crevices into which the eggs can roll, if eggs and larvae are to be protected.

The location of these suitable areas of bottom in the lake is primarily determined by currents or wave action which keep the bottom swept clean. The lake trout will roll the smaller stones around and fan off the silt, but they cannot remove sand or mud from the crevices. Any bottom that is not swept by currents or waves eventually becomes covered with mud, although in the usual oligotrophic lake-trout lake this process would take a very long time.

In the littoral zone, the width of the area of clean rocks or sand is dependent directly on the size of the lake and its exposure to the wind. In the smaller New York lakes the lake trout generally may be found spawning by windy points near deep water (Royce 1936), on bottom kept clean by the waves. A typical example of such shallow-water spawning is to be found in Otsego Lake.

In larger lakes the lake trout may go to deeper water for their spawning. Milner (1874) reports that the lake trout in Lake Superior spawn in 7 feet to 15 fathoms of water. Evidence of spawning in the deep water was provided by the capture of ripe fish at that depth and by raising in the nets fragments of honeycombed rocks containing eggs. In Seneca Lake the lake trout are captured for stripping in 100 to 200 feet of water at a time when no lake trout are found in shallow water. The fact that ripe lake trout are captured over bottom that is suitable for spawning is strong evidence that the trout actually are spawning at these depths. Further proof was provided by the capture on the spawning bed in Seneca Lake, in April 1940, of a lake-trout fry 25 millimeters in total length, in water 130 feet deep.

There is much evidence that these deeper spawning areas are swept by strong currents. The hatchery fishermen reported that their nets were often rolled over and over by the currents in Seneca Lake. In this same lake off Peach Orchard Point the 40° F. isotherm rose from a depth of 260 feet on September 29, 1941, to 100 feet on October 1 after a strong south wind; on October 7 it was back down to a depth of 230 feet. Such a change must be accompanied by the movement of a huge quantity of water.

These currents in Seneca Lake and the other Finger Lakes have left evidence of a prevailing direction of flow. All these lakes are very long and narrow and lie with their long axes in very nearly a north-south direction. Seneca Lake is the largest, being about 40 miles long and 3 miles wide at its widest point. The prevailing winds come from the northwest or the southeast, blowing obliquely to the south on the eastern shore and obliquely to the north on the western shore of the lake. The general result has been to form the tips of deltas to the south of the stream mouths on the eastern shore of the lake and to the north of the stream mouths on the western shore.

In addition to the characteristic orientation of the deltas, there is a definite gradation in the size of the material deposited in the various parts of the delta. Off the tip of Peach Orchard Point in Seneca Lake down to a depth of at least 300 feet, only clean gravel and rubble could be found with a clamshell dredge, or seen in bottom photo-

FIGURE 3.—The bottom of Seneca Lake west-southwest off the tip of Peach Orchard Point where the lake trout congregate during the spawning season. The picture covers an area on the bottom about 18 by 24 inches at a depth of 120 feet.

graphs [4] (fig. 3). The lighter materials, such as mud, were deposited in the coves adjacent to Peach Orchard Point.

Evidently other deltas in this lake have similar deposits, since lake trout are captured in large numbers during the spawning season near the tips of the points.

The writer has found no evidence that lake trout select a lake bottom supplied with spring water for the deposition of their eggs. The spawning area in Otsego Lake was on a fill about 100 feet out from the original shoreline which was bedrock and showed no evidence of any spring seepage. Comparison of numerous water temperatures taken on the spawning area and in the nearby lake at all seasons of the year showed no difference in temperature. Additional evidence was the presence of as thick an ice cover over the spawning area on March 31 as on other parts of the lake, just before the spring breakup, when any springs should have caused some erosion of the ice. No mention of spring water on lake-trout spawning areas has been found in the literature I have reviewed. It is concluded that for lake trout, unlike some other species of trout, spring water is a negligible factor in selection of a spawning area.

[4] Ewing, Vine, and Worzel (1946) describe submarine photographic equipment and techniques in detail.

SPAWNING ACT

All my observations on the spawning act of lake trout reported here were made at a spawning area on Otsego Lake, N. Y. Otsego Lake is about 8 miles long and averages three-fourths of a mile in width. Its maximum depth is 168 feet, and about 90 percent of the lake is more than 60 feet deep (Odell and Senning 1936). Chemical conditions are ideal for lake trout, and the lake has produced fairly good lake-trout fishing for

FIGURE 4.—The courtship act. The male at the left is nudging the female in the side.

many years. The spawning area kept under observation—the only one well known to the local residents and the only one that could be found—was along the middle of the west shore opposite the deepest part of the lake.

Observations were made in this area on November 16 and 30 and on December 1 and 5, 1940, and on December 1, 2, and 3, 1941. The trout were observed from 7 a. m. to 11 p. m. on some of those days, but the area was visited mostly in the evening.

Some trout were on the spawning area at all times of day during the spawning season, but most of the activity was restricted to the evening hours. During periods of bright sunlight only a few males could be seen and they kept to fairly deep water so that observation was difficult. The direct rays of the sun were cut off by a mountain about 4 p. m. and then many trout, both males and females, would arrive on the spawning area, and the males would start courtship and attempt the spawning act. The peak of the activity was from 5 p. m. to 9 p. m. Later in the evening the trout again disappeared until only a few were left at 11 p. m., when observations were discontinued.

No nest or redd was built. The males spent their time cruising along close to the bottom, occasionally giving the stones a little fillip with their tails, and several showed considerable abrasion on the lower jaw and under side of the tail from this fanning and digging. This activity cleaned several hundred square feet of bottom so thoroughly that it was easy to distinguish the area on which the trout were working even when they were not present.

It has been the experience of employees of the New York State Conservation Department in netting lake trout for spawn that the males appear in the nets on the spawning area earlier in the season than the females, and usually more males are caught. From this experience, and from the fact that the males predominated on the area in Otsego Lake, it seems probable that the males

FIGURE 5.—Just after completion of the spawning act. Two males have spawned with the female in the center.

are almost entirely responsible for any cleaning of the spawning area before spawning.

Belying their appearance, the males are not pugnacious. Occasionally one would make threatening motions at another male, but no vigorous fighting was observed. Several whitefish (*Coregonus clupeaformis*) and a large eel (*Anguilla bostoniensis*) were seen among the milling lake trout and were unmolested. It was noted, however, that the males were nearly of the same size. Perhaps they had already disposed of any venturesome small males.

Merriman (1935) and others have observed the spawning lake trout splashing at the surface. In Otsego Lake this was noted only infrequently, possibly because the spawning was on a steep slope in 2 to 15 feet of water—deeper water than that in which Merriman made his observations.

The males began their courtship upon the appearance of the females on the spawning area. Usually the male nudged the female in the side with his snout (fig. 4) and then attempted the spawning act. Frequently two or more males courted and attempted to spawn with a female at the same time. During courtship the males displayed the characteristic coloration (fig. 1) and commonly held the dorsal fin erect. These displays were apparently identical to those noted by Merriman (1935).

The spawning act or attempts at it normally consisted of one or two males approaching a female, pressing against her sides with their vents in close proximity and then quivering all over (fig. 5). Usually the mouths of both sexes were open and the dorsal fin of the male was held erect. This act was seen clearly at close range several times when no eggs or milt were expressed. On two occasions a cloudiness was noted in the vicinity of the vents which probably was caused by the emission of sperm. No eggs were seen but this could have been because of the distance of the observer from the fish and the turbidity of the water. No other act or behavior was seen which could be construed to accompany oviposition. Probably the attempt at the spawning act is a part of courtship and is repeated over and over again until fulfillment.

The spawning act was not limited to two or three trout; as many as seven males and three females were seen at one time, all pressing together in one large group and quivering in unison. No spawning act lasted for more than a few seconds, and it seems that a female must accomplish many unions to empty the ovaries completely. The trout are not monogamous and it was impossible to follow the movement of any one pair in the milling group.

No tendency toward oviposition in any definite place on the spawning area was observed. The trout mated at random over the area cleaned off, and there was no attempt by either sex to bury the eggs. This seeming carelessness in regard to the fate of their young was justified when one attempted to find the eggs. A casual examination of the bottom revealed practically no eggs, but they could be picked up by the hundreds when the stones were turned over carefully. Eggs were recovered in water from 3 inches to 14 feet in depth. Those collected in more than 2 feet of water had to be taken in a Petersen dredge and no estimate of their abundance could be obtained. Along shore in less than 2 feet of water, however, where only an occasional trout was seen spawning, from 20 to 50 eggs could be recovered per square foot of bottom. The eggs were difficult to pick up, and the slightest motion of the water sent them rolling further into crevices between the rocks. In their selection of the bottom on which to spawn, the lake trout had chosen an ideal shelter for their eggs and young.

ENVIRONMENT AND DEVELOPMENT OF EGGS AND LARVAE

EFFICIENCY OF FERTILIZATION

It has been a long-cherished belief of fish culturists that the natural spawning of trout is a highly inefficient, hit-or-miss process. Critical investigations have shown this belief to be untrue. White (1930) was able to hatch 79 percent of a sample of naturally fertilized brook-trout eggs removed from their redd and placed in a hatchery, and 66 percent of another lot placed in a screen basket and reburied in the redd. Hobbs (1937), after intensively investigating the redds of brown trout, rainbow trout, and quinnat salmon, found that more than 99 percent of the eggs were fertilized. He also found that subsequent heavy loss in the pre-eyed, eyed, and alevin stages was a result of adverse environmental conditions. Under favorable conditions the natural reproduction was a highly efficient process.

A check of the natural spawning of lake trout in Otsego Lake provided further evidence that natural reproduction is efficient. On December 28, 1941, about 25 days after the trout were observed on the spawning area, a sample of 309 eggs was collected from under the rocks along shore with a small rubber bulb and tube. Of these 309 eggs, 18, or 5.8 percent, were not fertilized, and 47, or 15.2 percent, had died. Seventy-nine percent of the eggs were alive and apparently entirely normal after having been on the lake bottom nearly a month. This probably represents a near minimum figure for the survival (exclusive of those eaten by predators) inasmuch as the eggs were of necessity collected in only a few inches of water where they were subject to heavy wave action. The vast majority of the eggs were laid in deeper water out of reach of available collecting apparatus and where they should have been better protected.

TEMPERATURE REQUIREMENTS

Lake-trout eggs appear both to require and to withstand slightly lower temperatures than the eggs of other trout. Embody (1934) found that brook- and rainbow-trout eggs suffered excessive mortality and developed at a different rate when the water temperature was below 37.4° F.[5] He found, also, that lake- and brown-trout eggs followed the same rate of development down to 35.2° F., and he judged that development proceeded normally. Brook trout usually spawn in spring water so that their eggs are not subjected to near-freezing temperatures during the winter (Greeley 1932, Hazzard 1932, White 1930). Rainbow trout normally spawn in the spring when the water is warming (Rayner 1941). Cook (1929) reports that lake-trout eggs develop satisfactorily at the Duluth, Minn., hatchery where water temperatures remain about 32.5° F. throughout the winter. The 140-day incubation period of lake-trout eggs in Otsego Lake indicates an average temperature of 36° or 37° F. in the egg-development tables of Embody (1934). At the Rome, N. Y., State hatchery high mortality occurred in lake-trout eggs developing at water temperatures above 50° F. when other trout eggs developed normally. In other hatcheries, lake-trout eggs from the same source developed normally at lower temperatures. These facts would indicate that lake-trout eggs can develop successfully in a lake in the winter, so long as they do not freeze, and that they do not require spring water.

No data are available on the temperature requirements of the alevins. In the spring of 1941 they left the spawning area in Otsego Lake when the water temperature was about 55° F. It seems likely, therefore, that they avoid temperatures above 60° F.

EFFECTS OF PREDATION

The data on the survival of eggs in Otsego Lake do not indicate the true value because they do not consider the removal of eggs by predators. Predators are an ever present danger to lake trout from the egg stage almost to maturity, and cause a loss which is exceedingly difficult to evaluate. No precise measurements have ever been made on the effects of predation at any stage in the growth of wild trout.

Many are the potential predators of eggs and alevins. Table 6 lists the animals captured within 100 yards of the lake-trout spawning area in Otsego Lake during April and May 1941. Many of these would destroy eggs if eggs were available to them. Atkinson (1931) and Greene, Hunter, and Senning (1932) found that numbers of lake-trout eggs were eaten by suckers (*Catostomus commersonii*) and bullheads (*Ameiurus nebulosus*). Both of these species occur in Otsego Lake although they were not captured in the immediate vicinity of the lake-trout spawning area. Greeley (1936) states that a fisherman reported finding lake-trout eggs in the stomachs of Otsego Lake whitefish. Rayner (1941) found many lake-trout eggs in the stomachs of adult lake trout. A female taken by the writer on the Otsego Lake spawning area had 13 lake-trout eggs in its stomach. Small lake trout may be even more voracious predators. W. C. Senning, in a letter to me, reported finding lake-trout eggs in every one of 31 small lake trout taken on the spawning grounds in Seneca Lake in the fall of 1942. These lake trout ranged from 6½ to 13 inches in length, and one 12-inch individual had eaten 147 eggs. White (1930) found large numbers of brook-trout eggs in brook-trout stomachs. Metzelaar (1929) reported that rainbow trout ate numbers of their own eggs. Greeley (1932) found brooks, browns, and rainbows to

[5] Rainbow-trout eggs suffered high mortality at temperatures below 43° F., but Embody thought that in some cases this was due to inferior eggs.

TABLE 6.—*Animals found on and near lake-trout spawning area in Otsego Lake, Apr. 27–June 2, 1941*

Phylum and order	Species	Common name	Stage
Coelenterata	*Hydra* sp.		
Platyhelminthes	*Planaria* sp.		
Arthropoda:			
Amphipoda	*Hyalella* sp.		
Neuroptera	*Sialis* sp.	Alderfly	Larva.
Ephemerida	*Blasturus* sp.	Mayflay	Nymph.
Do	*Ephemerella* sp.	do	Do.
Do	*Stenonema* sp.	do	Do.
Do	*Hexagenia* sp.	do	Do.
Do	*Ephemera* sp.	do	Do.
Odonata	*Gomphus* sp.	Dragonfly	Do.
Do	*Didymops transversa*	do	Do.
Do	*Epicordulia princeps*	do	Do.
Do	*Helocordulia uhleri*	do	Do.
Do	*Neurocordulia obsoleta*	do	Do.
Do	*Argia moesta*	Damsel fly	Do.
Do	*Enallagma* sp.	do	Do.
Plecoptera	*Neoperla* sp.	Stone fly	Do.
Coleoptera	*Dineutes* sp.	Whirligig-beetle	
Trichoptera	*Stenophylax scabripennis*	Caddisfly	Larva.
Do	*Molanna* sp.	do	Do.
Do	*Phryganea* sp.	do	Do.
Do	*Glossosomatinae* [1]	do	Do.
Diptera	*Chironomus* sp.	Midge	Do.
Do	*Tanytarsus* sp.	do	Do.
Mollusca:			
Gastropoda	*Limnea* sp.	Pond snail	
Do	*Planorbis* sp.	Wheel snail	
Pelecypoda	Unidentifiable	Clam	
Chordata:			
Pisces	*Coregonus clupeoformis*	Whitefish	
Do	*Cristivomer n. namaycush*	Lake trout	
Do	*Notropis h. hudsonius*	Spot-tail shiner	
Do	*Hyborhynchus notatus*	Blunt-nosed minnow.	
Do	*Esox niger*	Chain pickerel	
Do	*Anguilla bostoniensis*	American eel	
Do	*Perca flavescens*	Yellow perch	
Do	*Stizostedion v. vitreum*	Yellow pike-perch	
Do	*Bolesoma nigrum olmstedi*	Johnny darter	
Do	*Micropterus d. dolomieu*	Small-mouthed bass.	
Do	*Lepomis gibbosus*	Pumpkinseed (sunfish).	
Do	*Amblopliles rupestris*	Rock bass	
Do	*Cottus cognatus*	Slimy muddler	
Amphibia	*Triturus viridescens*	Newt	

[1] Two or more species.

be trout-egg eaters. On the Otsego Lake spawning area, an eel (*Anguilla bostoniensis*) and several whitefish (*Coregonus clupeaformis*) were seen industriously feeding among the stones where the lake trout were spawning. In addition, a slimy muddler (*Cottus cognatus*), which is known to eat trout eggs, was captured in the immediate vicinity.

What is the effect of this predation? Greeley (1932) concluded that practically all the eggs of rainbow, brown, and brook trout eaten were waste eggs not buried in the redd, and that the effect of egg predators on reproduction was negligible. Hobbs (1937) thought that the number of eggs eaten from the redds of rainbow and brown trout and quinnat salmon was very small. The spawning trout themselves are important predators but they could scarcely be accused of eating all their own spawn.

It seems likely that predation would have no more effect on the eggs of lake trout than it has on those of other trout. If the lake trout can spawn on the type of bottom they seem to prefer, the eggs and alevins are certainly well protected until they emerge from the rubble. It was necessary to dig deep into the rubble in the Otsego Lake spawning area to capture either eggs or alevins.

Additional evidence is provided by the lack of any lake-trout alevins in the stomachs of the following fish captured in the immediate vicinity of the lake-trout spawning area between April 27 and June 2, 1941:

6 whitefish (*Coregonus clupeaformis*)
1 adult lake trout (*Salvelinus* [=*Cristivomer*] *namaycush*)
11 shiners (*Notropis hudsonius*)
1 blunt-nosed minnow (*Hyborhynchus notatus*)
1 chain pickerel (*Esox niger*)
17 yellow perch (*Perca flavescens*)
22 johnny darters (*Boleosoma nigrum olmstedi*)
1 smallmouth bass (*Micropterus d. dolomieu*)
4 common sunfish (*Lepomis gibbosus*)
13 rock bass (*Ambloplites rupestris*)
11 slimy muddlers (*Cottus cognatus*)

These fish were all captured during the presumably vulnerable time the alevins were absorbing the yolk sac and leaving the spawning bed. Such negative evidence is inconclusive but reassuring.

It is important to note that most trout-egg predators have been indicted for their activities during the time the eggs were being laid and not after the eggs were hidden in the gravel. It is concluded that lake-trout eggs and alevins suffer little from predation after the spawning season, and that during spawning the eggs that are eaten are only those left exposed on the bottom.

DEVELOPMENT OF EGGS AND ALEVINS

Greeley (1936) collected eyed eggs and newly hatched alevins on the Otsego Lake spawning area on April 12, and more-advanced alevins on May 9. I took newly eyed eggs on February 17, 1941, and later-eyed stages on March 31, 1941, by chopping holes through the ice. (The lake trout had been observed spawning December 5, 1940.) Later, on April 27, with the surface water temperature 44° F., newly hatched sac fry were taken, and on May 17, 1941, many more-advanced fry were taken (temperature data in fig. 6). All the stages were taken from the rubble on the spawning area.

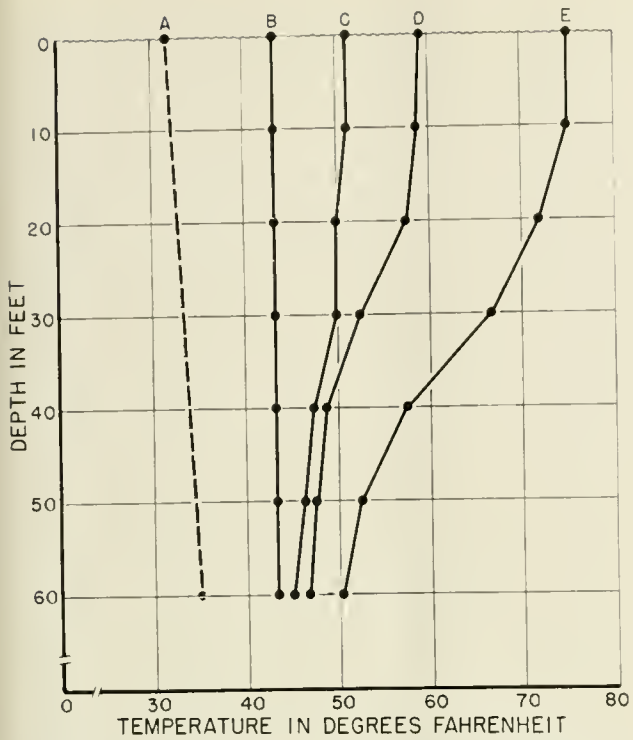

FIGURE 6.—Temperature stratification of Otsego Lake associated with different stages of larval development of lake trout.

(Several hauls of the trawl in the vicinity of the spawning area on April 27 and May 17 produced no fry.) Both eggs and fry were well buried in the stones. The eggs were taken with a Petersen dredge, and only after the surface stones were removed could they be found. The fry were all taken with a trawl fitted with a heavy weight in front which turned over the stones. On June 2, 1941, 18 tows of the trawl over the spawning area and in the vicinity down to depth of 60 feet failed to produce any young lake trout. They had definitely moved from the spawning area and the habitat of the earliest feeding stages was still unknown.

Comparison of the development of wild fry which were captured and of those grown in a hatchery indicates that the time of hatching in Otsego Lake in 1941 was about April 15, and the fry left the shelter of the spawning area May 20 to 25.

In Seneca Lake, where the lake trout spawn during late September and October, a single advanced fry was captured in about 130 feet of water off Peach Orchard Point on April 2, 1940. This fry was considerably more advanced than a hatchery fry 2 months old. This would place the time of hatching in late January and indicate an incubation period of approximately 4 months.

Consideration of the type of bottom and the kinds of invertebrate inhabitants (table 6) of the lake-trout spawning area in Otsego Lake emphasizes the striking resemblance of this area to a typical trout-stream environment. Clean gravel and rubble bottom inhabited by stonefly and mayfly nymphs and caddis larvae ordinarily would be associated with a stream instead of a lake. Certainly it seems that lake-trout fry and fingerlings would fare best under conditions similar to those selected by the young of other trout.

This trout-stream-like environment in Otsego Lake gave me high hopes of capturing the early fingerling stages in the vicinity. But all efforts, including those with minnow traps, trawl, and shore seine, were unsuccessful. No helpful clues were found in the literature, for lake-trout fingerlings have been reported only from shoal water and small tributaries. Kendall and Goldsborough (1908) captured several lake trout, 1.87 to 2.37 inches long, in small spring tributaries of First Connecticut Lake on July 16 and 18 and August 10. Neave and Bajkov (1929) reported taking 10 lake trout, 32 to 45 mm. long, with a hand net in a small inlet creek at Pyramid Lake, Nev. Miller and Kennedy (1948) noted that fry, and 1-, 2-, and 3-year-old lake trout were found in shallow water along a bouldery shoreline of Great Bear Lake, Mackenzie, Canada. Lake-trout fingerlings are not found in such habitats in the summer in New York. The biological survey of the New York State Conservation Department captured none in extensive seining of the shores of the Adirondack lakes and streams, many of which were adjacent to lake-trout waters. There seems to be little doubt that in New York they live in the deeper waters of the lakes in the summer and probably seek rocky bottom.

JUVENILE LAKE TROUT OF KEUKA LAKE

Intermittently from April 18 to September 16, 1940, effort was made to capture fingerling and juvenile stages of lake trout in Keuka Lake. Their capture was attempted with gill nets, trawls, set lines, and minnow traps. A number of 100-foot sections of gill nets of ⅝-inch to 1½-inch bars were set for an aggregate of 67 nights at depths of

10 to 130 feet. Fifty-nine tows of a trawl were made over a similar range of depths. A set line equipped with 80 No. 7 hooks was set for 4 days covering depths from 15 to 40 feet. Minnow traps were set for 8 days at depths from 40 to 80 feet.

Included in the catch were 41 lake trout (all caught in gill nets) of which 13 were more than 15 inches in total length—the minimum legal size in New York. The stomach content of the 13 legal-sized trout, and of 11 others of legal size gathered from anglers, was 100 percent alewives (*Pomolobus pseudoharengus*) or unidentifiable fish, probably of the same species (anglers report finding practically nothing but alewives in lake-trout stomachs).

The lengths and stomach contents of the sublegal specimens are listed in table 7. Of the 16 specimens between 10 and 15 inches in length, only one had eaten arthropods, while the principal food of those between 6 and 10 inches was arthropods, mostly *Mysis relicta*.

TABLE 7.—*Food of lake trout less than 15 inches long from Keuka Lake, 1940*

Total length (inches)	Date of capture	Stomach contents
14⅞	May 11	Empty.
14¼	do	Unidentifiable fish remains.
14	do	3 *Pomolobus pseudoharengus;* 2 unidentifiable fish.
13¾	do	2 *Pomolobus pseudoharengus.*
13	do	4 *Cottus cognatus.*
12⅞	do	Unidentifiable fish remains.
12½	June 29	Do.
12⅛	May 11	Do.
11¼	June 29	Do.
11¼	May 24	Do.
11⅛	do	Do.
10⅞	May 11	Do.
10¾	do	Empty.
10⅜	do	Unidentifiable fish remains.
10⅜	Sept. 11	1 mayfly nymph (Ephemerinae); 1 unidentifiable fish.
10¼	May 25	5 *Pomolobus pseudoharengus.*
9⅞	Sept. 13-16	1 *Pungitius pungitius;* 23 *Mysis relicta.*
9⅝	May 24	Unidentifiable fish remains.
9½	Sept. 13-16	1 *Pungitius pungitius;* 1 unidentifiable fish.
7⅞	do	1 *Cottus cognatus;* 9 *Mysis relicta.*
7⅞	do	12 *Mysis relicta.*
7½	do	16 *Mysis relicta.*
7½	do	34 *Mysis relicta.*
7⅛	do	25 *Mysis relicta.*
6⅞	do	10 *Mysis relicta.*
6¾	do	20 *Mysis relicta.*
6¾	do	19 *Mysis relicta.*
6½	do	28 *Mysis relicta.*

SUMMARY: Of lake trout 10 to 15 inches in total length, 14 stomachs contained fish remains and 1 stomach contained arthropod remains. Of lake trout 6 to 10 inches in total length, 4 stomachs contained fish remains and 10 stomachs contained arthropod remains.

In most cases capture of the lake trout was very erratic. The 10 small specimens taken May 11 were found in the same place at very nearly the same depth of 100 feet. Nets set there on following nights caught nothing. The other small specimens taken during May and June and all the larger lake trout were caught, one or two at a time, in different places but almost entirely at depths of 80 to 120 feet.

Some consistency was found, however, in the capture of the young lake trout caught September 11 to 16, 1940. These were taken, two or three a night, in ⅝- to ¾-inch bar gill nets set in one restricted location off the southern tip of Bluff Point, a very rocky, steep underwater slope, between depths of 40 and 70 feet. Nets of the same mesh set at the same depths in the vicinity on mixed mud and rubble bottom failed to catch any trout. As large lake trout were taken in larger-mesh nets in the same area, it seems that the juveniles must have been relying on the shelter of the rocks for protection from their voracious elders.

Scale examination indicated that these 6½- to 10-inch trout were yearlings and 2-year-olds. Since the lake trout of Keuka Lake spawn in late November and probably hatch in late April (see p. 64, table 5), a rate of growth comparable to hatchery growth would allow them to reach only 2 or 3 inches by the first September. Possibly these fingerling fish could be found in the same location as the yearlings were found. Lack of time and equipment prevented any further effort in this direction but it is a good stage at which to resume the search in the future.

SUMMARY

Lake trout were observed during their spawning season in 1939, 1940, and 1941 in several lakes in New York State, and actual spawning was seen in Otsego Lake, N. Y. Extensive data on spawn-taking operations were obtained from the New York State Conservation Department, and existing literature on the subject was reviewed.

It was found that, except for a striking color change in the males while on the spawning area, lake trout lack sexual dimorphism. They mature in about their sixth year at lengths varying from 15 to 30 inches in the different lakes.

Spawning occurs once each year, during the autumn. The date varies from late September to early December depending on the race of trout, the amount of sunlight, the autumnal drop in temperature, and the depth of the lake.

In the deep water of Seneca Lake, one race

spawned early. In all other lakes studied, the lake trout spawned in shallow water and usually later. Increased cloudiness in July, August, and September, and low temperatures in September, advanced the date of spawning in Raquette Lake. Shallower lakes had earlier spawning dates. At the time of spawning, water temperature varied from 58° to 37° F., but in Raquette and Otsego Lakes it was observed that spawning times approximated the turn-over times of the lakes. Generally, the spawning period was about 20 days, but it varied from 10 to 40 days and was fairly consistent from year to year in any one lake.

Spawning, whether in shallow or deep water, took place on gravel or rubble bottom that had crevices into which the eggs could roll. No nest or redd was built. No evidence of spring water was observed near any spawning area.

In the spawning act, which usually occurred during the evening, from 2 to 10 lake trout participated. Each attempt at spawning lasted only a few seconds; the act was repeated many times.

Approximately 1 month after spawning, a sample of eggs recovered from the crevices in the rocks of Otsego Lake was found to be 79 percent alive. No measurement of the effects of predation on eggs was possible, but it was estimated that only eggs that failed to roll into crevices between the stones could be eaten by predators.

In Otsego Lake in 1941 the eggs hatched about April 15 and the fry left the spawning area about May 22. In the deep water of Seneca Lake where the lake trout had spawned in early October a single advanced fry was taken April 2, 1940. Its development indicated that hatching occurred in late January.

Extensive operation of a small beam trawl, set lines, and minnow traps in Otsego, Keuka, and Seneca Lakes failed to produce any lake trout between advanced fry stage and a length of about 6 inches. Twelve specimens between 6 and 10 inches long that were captured in gill nets in Keuka Lake were found to be 1- and 2-year-olds and to be feeding mostly on *Mysis relicta*.

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DECLINE OF THE LAKE TROUT FISHERY IN LAKE MICHIGAN

By RALPH HILE, PAUL H. ESCHMEYER, and GEORGE F. LUNGER

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CONTENTS

	Page
Materials and methods	77
Production trends in Lake Michigan, 1879–1949	78
Production in State of Michigan waters, 1891–1908 and 1929–49	81
Abundance in State of Michigan waters, 1929–49	88
Fishing intensity in State of Michigan waters, 1929–49	90
Relations of production, abundance, and fishing intensity	92
Summary	94
Literature cited	95

DECLINE OF THE LAKE TROUT FISHERY IN LAKE MICHIGAN

By RALPH HILE and PAUL H. ESCHMEYER, *Fishery Research Biologists*, and GEORGE F. LUNGER, *Statistician*

Collapse of the fishery for lake trout, *Salvelinus* [=*Cristivomer*] *namaycush*, of Lake Huron has been treated in detail in a recent publication by Hile (1949). In the present paper we take up the unpleasant task of describing the decline of the lake-trout fishery in yet another of the Great Lakes, Lake Michigan. Lake Superior now stands as the only significant center of commercial production of that species yet remaining in the United States.

In this, as in the earlier paper mentioned, treatment will be limited to a statistical account of the changes that have taken place in the lake-trout fishery. We offer no extended argument on the role of the sea lamprey in this most recent debacle, other than to express the considered opinion that on the basis of currently available evidence this parasite must be held the major cause of the catastrophes that have overtaken both Lake Huron and Lake Michigan.

MATERIALS AND METHODS

The statistics on the production of lake trout in the individual States over the period 1879–1940, incorporated in table 1, were adapted from Gallagher and Van Oosten (1943) and are from the sources listed in that publication. Our annual totals, however, are in agreement with those of Gallagher and Van Oosten only for those years in which statistics were available for all four States bordering the lake. In a number of years statistics were at hand for Michigan and Wisconsin but not for Illinois and Indiana; in such situations those authors recorded the yields from the first two States as the totals for Lake Michigan. Our totals in the same situations include estimates of the Illinois-Indiana catch. On the basis of the actual distribution of the take among the States in the 8 years with complete data from 1885 through 1917 and in the 6 years [1] from 1922 through 1929 we derived the correction factors 1.0291 and 1.0683. The former factor was applied to the combined Michigan-Wisconsin catch to give an adjusted grand total in years lacking Illinois-Indiana data through 1919; the latter factor was used for years after 1919. To be sure, the percentage contribution of Illinois and Indiana varied within each of the two periods, but the derivation of a greater number of factors would not have been profitable. We have not considered it advisable to estimate the Lake Michigan total in any year for which we had data for only one State.

Statistics on production after 1940 were compiled directly from commercial fishermen's reports in the Ann Arbor offices of the Fish and Wildlife Service (Michigan) or supplied by State conservation agencies (Wisconsin, Illinois, and Indiana).

The data on the yield of lake trout in the several statistical districts of the State of Michigan waters of Lake Michigan for 1891–1908 were tabulated in the Service's Great Lakes offices from original records supplied by the Michigan Department of Conservation.[2]

The detailed information on production, fishing intensity, and estimated availability of lake trout in the State of Michigan waters in 1929–49 is based on analyses of monthly reports of commercial fishermen licensed by the State of Michigan. These reports, which were supplied by the department of conservation, contain data on fishing locality, kind and amount of gear fished, and kinds and quantities of fish captured for each day of fishing by each licensee.

The methods employed in estimating the abundance of the principal species and the intensity of the fishery in the State of Michigan waters of the Great Lakes have been described in detail in earlier publications (Hile 1937; Hile and Jobes

[1] For this purpose the 1925 data were usable since the Indiana-Illinois catch was included in the total; statistics for the two States individually, however, were not available.

[2] The Works Progress Administration gave valuable assistance in this work.

1941; Van Oosten, Hile, and Jobes 1946). The boundaries of the eight statistical districts, M–1 to M–8, are given in figure 2.

PRODUCTION TRENDS IN LAKE MICHIGAN, 1879–1949

The trends of production of lake trout from 1879 through 1949 perhaps can be brought out best through comments on the yield over certain periods of years (tables 1 and 2; fig. 1).

The take in 1879, the first year for which we have a record, was comparatively low (2,659,000 pounds). Catches were higher in 1885 (6,431,000 pounds) and 1889 (5,580,000 pounds) but the take in each of those years and the mean for the two (6,006,000 pounds) were far below the level that characterized the period beginning with 1890. It may be assumed that the fishery was in the process of development in 1879–89.

The interval 1890–1911 was one of rather consistently high production. The take exceeded 8 million pounds in 7 of the 11 years for which lake totals are recorded and was more than 9 million pounds in 1 of these 7 (9,282,000 pounds in 1896). Of the remaining 4 years, 2 had yields between 7 and 8 million pounds, 1 between 6 and 7 million, and 1 less than 6 million. The two lowest catches (6,624,000 pounds in 1892 and 5,286,000 pounds in 1899) both deviated sharply from the general level for the period and both can be attributed to the low yields recorded for Wisconsin. The grand average catch [3] for 1890–1911 was 8,230,000 pounds or 2,224,000 pounds greater than for 1885–89. Every State but Indiana shared in the increase; the rise was greatest, however, in Wisconsin (1,950,000 pounds).

The production of lake trout in Lake Michigan was at a decidedly lower level in 1912–26 when the average yield of 7,007,000 pounds was 1,223,000 pounds below that of 1890–1911. Of the 14 years for which there are totals (see footnote 1 to table 1 concerning the exclusion of data for Wisconsin in 1921) 5 had catches between 7 and 8 million pounds, 8 between 6 and 7 million pounds, and 1 less than 6 million pounds. The highest yield was 7,928,000 pounds in 1915 and the lowest was 5,979,000 pounds in 1918. Declines from the preceding period of 932,000 pounds in Wisconsin and 459,000 pounds in Michigan, were compensated to a small degree by increases of 132,000 pounds in Indiana and 36,000 pounds in Illinois.

[3] To obtain full use of the data of table 1, the means in the body of table 2 were determined from all records of yield for each State during the indicated periods and these State means were added to obtain the totals at the right.

TABLE 1.—*Production of lake trout in Lake Michigan, 1879–1949*

[In thousands of pounds]

Year	State				Total
	Michigan	Wisconsin	Illinois	Indiana	
1879					2,659
1880					
1881					
1882					
1883					
1884					
1885	3,725	2,668	4	34	6,431
1886					
1887					
1888					
1889	2,950	2,455	25	150	5,580
1890	4,674	3,464	72	155	8,364
1891	3,686				
1892	3,616	2,821			6,624
1893	3,122	5,404			8,774
1894	2,668	5,865			8,781
1895	2,392	5,304			7,920
1896	3,020	6,000			9,282
1897	2,872	4,711	219	21	7,823
1898	2,540				
1899	2,370	2,804	77	35	5,286
1900	2,016				
1901	2,844				
1902	4,337				
1903	4,055	4,613	199	76	8,943
1904	4,254				
1905	4,456				
1906	5,103				
1907	4,271				
1908	4,023	4,328	150	130	8,631
1909		4,371			
1910		4,337			
1911	3,526	4,640			8,404
1912	3,003	3,558			6,752
1913	2,544	3,761			6,488
1914	2,711	4,126			7,036
1915	3,853	3,851			7,928
1916	2,805	3,195			6,174
1917	2,866	3,745	169	123	6,904
1918	2,456	3,354			5,979
1919	2,735	3,849			6,776
1920	3,143	3,840			7,461
1921	3,107	[1] 8,642			[1] 12,551
1922	3,264	3,801	203	272	7,540
1923	2,757	3,419			6,599
1924	3,472	3,752			7,717
1925	3,422	3,101			[2] 6,894
1926	3,352	2,762	165	250	6,530
1927	2,900	2,379	167	253	5,699
1928	1,831	2,629	172	187	4,819
1929	2,198	3,817	247	132	6,394
1930	2,556	2,316	383	186	5,441
1931	2,652	2,673	202	106	5,632
1932	2,746	2,345	281	98	5,470
1933	2,379	2,481	262	90	5,212
1934	2,053	2,590	225	88	4,957
1935	2,451	2,042	260	120	4,873
1936	2,127	2,232	274	130	4,763
1937	2,264	2,353	271	100	4,988
1938	2,480	1,940	311	174	4,906
1939	2,778	2,358	318	205	5,660
1940	2,780	2,492	814	179	6,266
1941	3,189	2,747	705	146	6,787
1942	2,641	2,695	1,111	38	6,484
1943	2,814	2,825	1,193	28	6,860
1944	2,609	2,852	1,036	[2]	6,498
1945	2,228	2,516	694	[2]	5,437
1946	1,908	1,650	416	1	3,974
1947	914	1,178	333	1	2,425
1948	589	542	65	[3]	1,197
1949	223	115	4		342

[1] The recorded yield of 8,642,000 pounds in Wisconsin in 1921 is so badly out of line with data for neighboring years as to be held unreliable. It was not plotted in fig. 1 or employed in the computation of any means or percentages.

[2] No breakdown available of the 371,000 pounds taken in Indiana and Illinois.

[3] Less than 500 pounds.

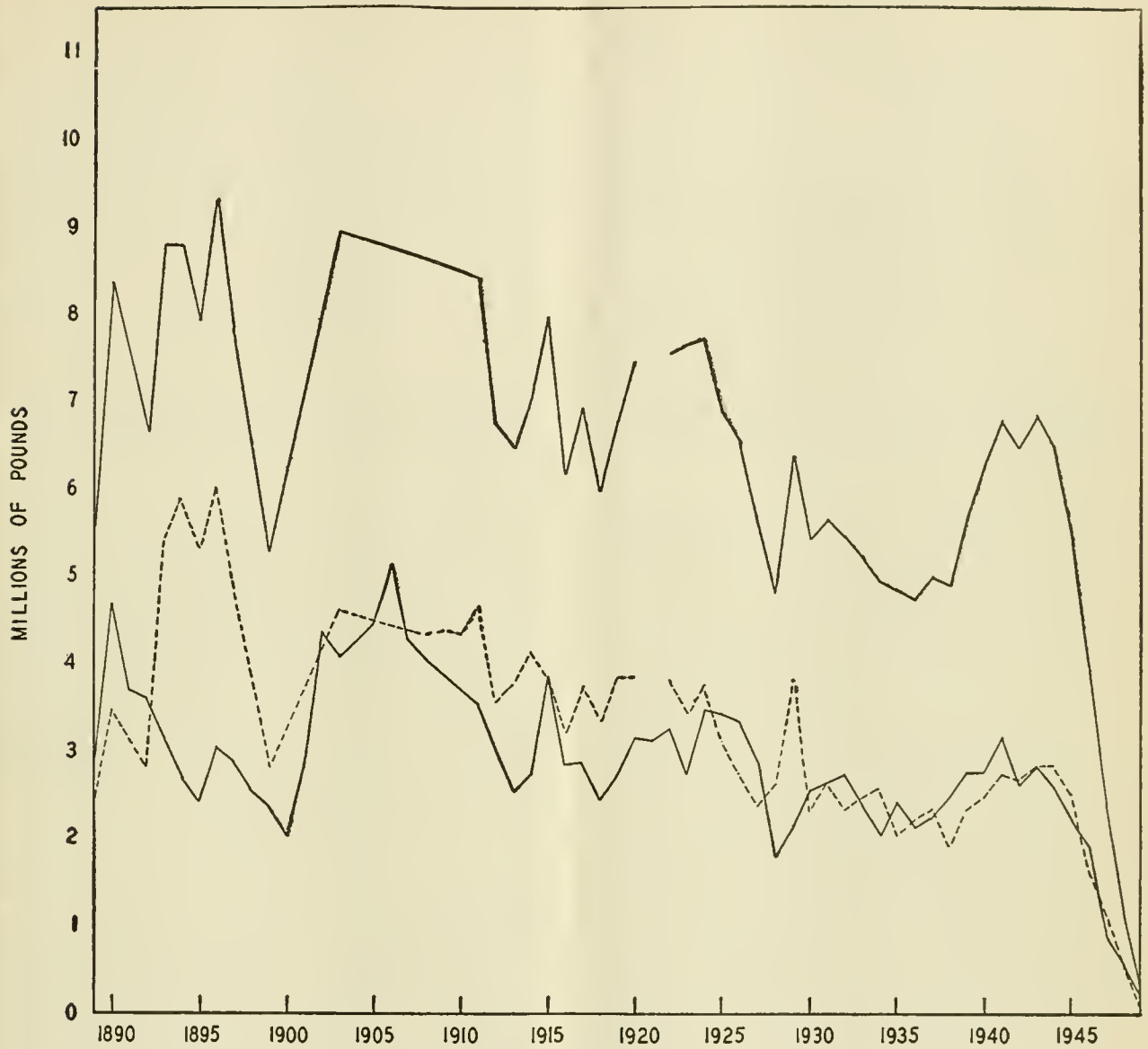

FIGURE 1.—Production of lake trout in Lake Michigan, 1889–1949. Upper solid line=entire lake; broken line=Wisconsin; lower solid line=Michigan.

The take of lake trout fluctuated about a still lower level in 1927–39 when the average total for the lake was 5,293,000 pounds, 1,714,000 pounds below the mean for 1912–26 and 2,937,000 pounds less than that for 1890–1911. The catch exceeded 6 million pounds only once in 13 years (6,394,000 pounds in 1929—again a sharp deviation of the Wisconsin figure from the characteristic level was responsible for the extreme); it was between 5 and 6 million pounds in 6 years, and less than 5 million pounds in 6 years. The lowest catch of the period was 4,763,000 pounds in 1936. Michigan, Wisconsin, and Indiana contributed to the decline from 1912–26 to 1927–39 with decreases of 616,000, 1,107,000, and 71,000 pounds, respectively. The Illinois catch, on the contrary, was increased by 80,000 pounds in the latter period.

The lake-trout fishery of Lake Michigan enjoyed a brief period of heightened productivity in 1940–44 when the take exceeded 6 million pounds in every one of the 5 years and averaged 6,578,000 pounds, or 1,285,000 pounds above the 1927–39 mean. To a considerable extent the improvement can be attributed to the large increase of 713,000

TABLE 2.—*Average production of lake trout in Lake Michigan, by periods*

[In thousands of pounds]

Period	Number of years [1]	Item	State				Total
			Michigan	Wisconsin	Illinois	Indiana	
1879	1	Production					2,659
1885–89	2	Mean annual production	3,338	2,562	14	92	6,006
		Percentage of total	55.6	42.7	0.2	1.5	100
1890–1911	22	Mean annual production	3,492	[2] 4,512	143	83	8,230
		Percentage of total	42.4	54.8	1.8	1.0	100
1912–26	15	Mean annual production	3,033	[3] 3,580	179	215	7,007
		Percentage of total	43.3	51.1	2.5	3.1	100
1927–39	13	Mean annual production	2,417	[4] 2,473	259	144	5,293
		Percentage of total	45.7	46.7	4.9	2.7	100
1940–44	5	Mean annual production	2,807	2,722	972	78	6,578
		Percentage of total	42.7	41.4	14.7	1.2	100
1945–49	5	Mean annual production	1,172	1,200	302	0	2,674
		Percentage of total	43.8	44.9	11.3	0	100

[1] Number of years for which statistics were available in at least 1 State or for the entire lake.

[2] The reported Wisconsin production for the years 1892 and 1899 was far below the level characteristic of the period. If these years are excluded, the Wisconsin mean becomes 4,822 and the percentages and total change accordingly.

[3] Excluding 1921 for which year the reliability of the Wisconsin data appears questionable.

[4] The reported Wisconsin production for 1929 was considerably above the level characteristic of the period. If this year is excluded, the Wisconsin mean becomes 2,362 and the percentages and total change accordingly.

pounds in Illinois, a rise exceeding the combined increases in Michigan (390,000 pounds) and Wisconsin (249,000 pounds). Indiana alone experienced a decline (66,000 pounds).

The sharp drop in the recorded Indiana take to a lower level during the 1940–44 interval probably reflects improvement in the collection of statistics more than a decrease in output. Indiana producers, who traditionally take the bulk of their catch of lake trout in State of Michigan waters, have to our best knowledge customarily reported their entire production to both Indiana and Michigan. There is considerable evidence, therefore, that part of the take of Indiana fishermen in earlier years was reported in duplicate. In view of the relatively small production of these operators, the effects on the statistics for the entire lake were not particularly damaging, but the figures for Indiana before about 1942 must be viewed with some skepticism.

The period 1940–44 is exceptional for its brevity. Statistics for the preceding three periods demonstrated a tendency for the productivity of the lake-trout fishery to fluctuate closely about a characteristic level for from 13 to 22 years. In view of this tendency, it might well be expected that the new high level reached in 1940 would be maintained longer than 5 years. That it was not maintained suggests that some disruptive factor intervened. The sea lamprey qualifies well as that factor.

Although the downward trend of production actually started a year earlier, 1945 can be set a the beginning year of the recent disastrous decline. In this year the catch dropped by more than a million pounds and fell distinctly below the level of 1940–44. Once the decline started, its progress was spectacular. In 1946 the take was under 4 million pounds for the first time since 1879, and each of the years 1947 to 1949 set a new record low. It is the high rate of decrease rather than the average of 2,674,000 pounds that makes the 1945–49 period significant.

The collapse of production in the lake-trout fishery of Lake Michigan resembles closely that described for Lake Huron by Hile (1949). Indeed, the decline appears to have been even more rapid in Lake Michigan than in the United States waters of Lake Huron. This point can be brought out by a comparison of the number of years required for a 90-percent or greater decline from the last year with the take above the "modern" average. In Lake Michigan this average can be set at 5,651,000 pounds (the mean for 1927–44), and the last year in which the take exceeded that figure was 1944 (6,498,000 pounds); only 5 years later the catch had dropped by 94.7 percent (to 342,000 pounds in 1949). In the United States waters of Lake Huron the "modern normal yield" was set by Hile at 1,685,000 pounds (the mean for 1895–1939), and the last year with an output above this figure was 1935 (1,743,000 pounds); 10 years were required for the catch to decline 90.1 percent (to 173,000 pounds in 1945).

PRODUCTION IN STATE OF MICHIGAN WATERS, 1891–1908 AND 1929–49

Records of the annual take of lake trout in the several statistical districts [4] of the State of Michigan in 1891–1908 (table 3) make possible the comparison of the actual productivity of various regions and of their percentage contributions to the total for the lake [5] in that period with conditions in recent years (table 4). Despite the considerable fluctuations in annual yield in the different districts to be seen in table 3, comments on the 1891–1908 data [6] will be restricted to the averages; we are without the information on fluctuations in the availability of lake trout, in the intensity of the fishery, and in other conditions, that we need for an intelligent treatment of the matter. Attention should be called, however, to the distinct similarity of trends in production in the several districts.

TABLE 3.—*Production of lake trout in Michigan statistical districts, 1891–1908*

[In thousands of pounds]

Year	District								Total
	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8	
1891	171	349	1,554	130	346	228	395	513	3,686
1892	35	390	1,691	77	379	290	257	496	3,616
1893	174	144	1,392	98	311	318	360	324	3,122
1894	142	249	1,285	86	255	224	185	243	2,668
1895	109	57	1,312	118	267	185	165	180	2,392
1896	119	392	1,529	151	307	207	160	155	3,020
1897	176	411	1,456	76	212	200	174	167	2,872
1898	161	288	1,367	46	233	258	98	89	2,540
1899	127	264	1,160	47	298	190	130	154	2,370
1900	90	191	782	42	259	190	195	266	2,016
1901	168	361	1,073	78	330	344	212	279	2,844
1902	307	470	1,704	112	362	345	542	493	4,337
1903	380	598	1,534	94	422	246	368	412	4,055
1904	363	572	1,708	138	428	311	296	438	4,254
1905	382	538	1,903	158	443	380	238	412	4,456
1906	332	348	2,325	195	498	503	446	456	5,103
1907	299	298	1,670	170	437	446	503	448	4,271
1908	300	421	1,553	134	330	483	484	318	4,023
1891–1908 mean	213	352	1,500	108	340	297	289	325	3,425
Percentage of total	6.2	10.3	43.8	3.2	9.9	8.7	8.4	9.5	100

TABLE 4.—*Production of lake trout in Michigan statistical districts, 1929–49*

[In thousands of pounds]

Year	District								Total	Production index [1]
	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8		
1929	182	153	912	68	273	291	146	174	2,198	86
1930	203	234	986	90	286	270	224	262	2,556	101
1931	220	300	1,020	102	321	291	249	148	2,652	104
1932	194	331	898	113	387	354	313	156	2,746	108
1933	134	298	692	102	449	303	206	196	2,379	94
1934	72	276	669	71	380	278	144	163	2,053	81
1935	77	242	771	89	432	306	234	300	2,451	96
1936	158	259	823	76	363	143	111	193	2,127	84
1937	236	296	738	88	447	147	131	180	2,264	89
1938	248	243	801	117	437	183	148	303	2,480	98
1939	157	234	1,047	100	407	266	195	370	2,778	109
1940	83	220	739	109	427	424	289	488	2,780	109
1941	75	354	910	141	449	413	414	432	3,189	126
1942	56	251	684	133	385	283	342	508	2,641	104
1943	91	299	837	122	453	274	216	523	2,814	111
1929–43 mean	146	266	835	101	393	282	224	293	2,540	100
Percentage of total	5.7	10.5	32.9	4.0	15.5	11.1	8.8	11.5	100	
1944	47	195	675	131	462	251	261	587	2,609	103
1945	29	145	599	96	299	227	247	586	2,228	88
1946	11	79	448	68	263	152	293	593	1,908	75
1947	46	25	219	38	126	71	155	234	914	36
1948	178	25	87	19	86	19	45	131	589	23
1949	149	3	23	13	21	5	2	6	223	9

[1] Percentage of 1929–43 mean.

Despite the considerable fluctuations in annual yield in the different districts to be seen in table 3, comments on the 1891–1908 data [6] will be restricted to the averages; we are without the information on fluctuations in the availability of lake trout, in the intensity of the fishery, and in other conditions, that we need for an intelligent treatment of the matter. Attention should be called, however, to the distinct similarity of trends in production in the several districts.

District M–3 strongly dominated the production of lake trout in the State of Michigan waters of Lake Michigan in 1891–1908, contributing 43.8 percent of the total output for the period. The percentages for five of the seven remaining districts exhibited only small differences, ranging from 10.3 percent for M–2 which held second position to 8.4 percent for M–7 which ranked sixth. The lowest average yields were in M–1 (6.2 percent) and M–4 (3.2 percent). In this early period, waters north of Grand Traverse Point (M–1, M–2, and M–3) accounted for 60.3 percent of the total output as compared with 39.7 percent for districts M–4 through M–8.

To facilitate comparisons between the production of lake trout in the statistical districts in 1891–1908 (table 3) and 1929–43, the "base period" for modern statistics (table 4), a summary (table 5) has been prepared. The principal features of the comparison are a generally lower level of take in the more recent period, a shifting of production toward the more southerly districts, and a lack of pronounced changes in the ranking of the districts with respect to the percentage of total yield.

Only M–5 exhibited a rise in average annual production from 1891–1908 to 1929–43 (an increase of 53,000 pounds). The remaining seven districts all suffered declines that ranged from 7,000 pounds in M–4 to the tremendous drop of 665,000 pounds in M–3. This latter decline accounted for most of the decrease of 885,000 pounds for the combined districts. In no other district did the take fall by more than 86,000 pounds (the decrease for M–2).

[4] See figure 2 for the boundaries of the statistical districts.

[5] The term "lake" in this and the following sections has reference to State of Michigan waters only.

[6] The data for 1891–1908 provide a less reliable record of production in the individual districts than do those for 1929 and later. In the earlier period the annual catch of each fisherman was allocated to the district in which his home port was located, whereas in the recent period each day's catch was credited to the statistical district in which the gear actually was lifted. The extent to which fishermen operated outside their home districts in 1891–1908 is unknown, but records for recent years suggest that error from this source was not sufficiently great to affect the validity of comparisons based on tables 3 and 4.

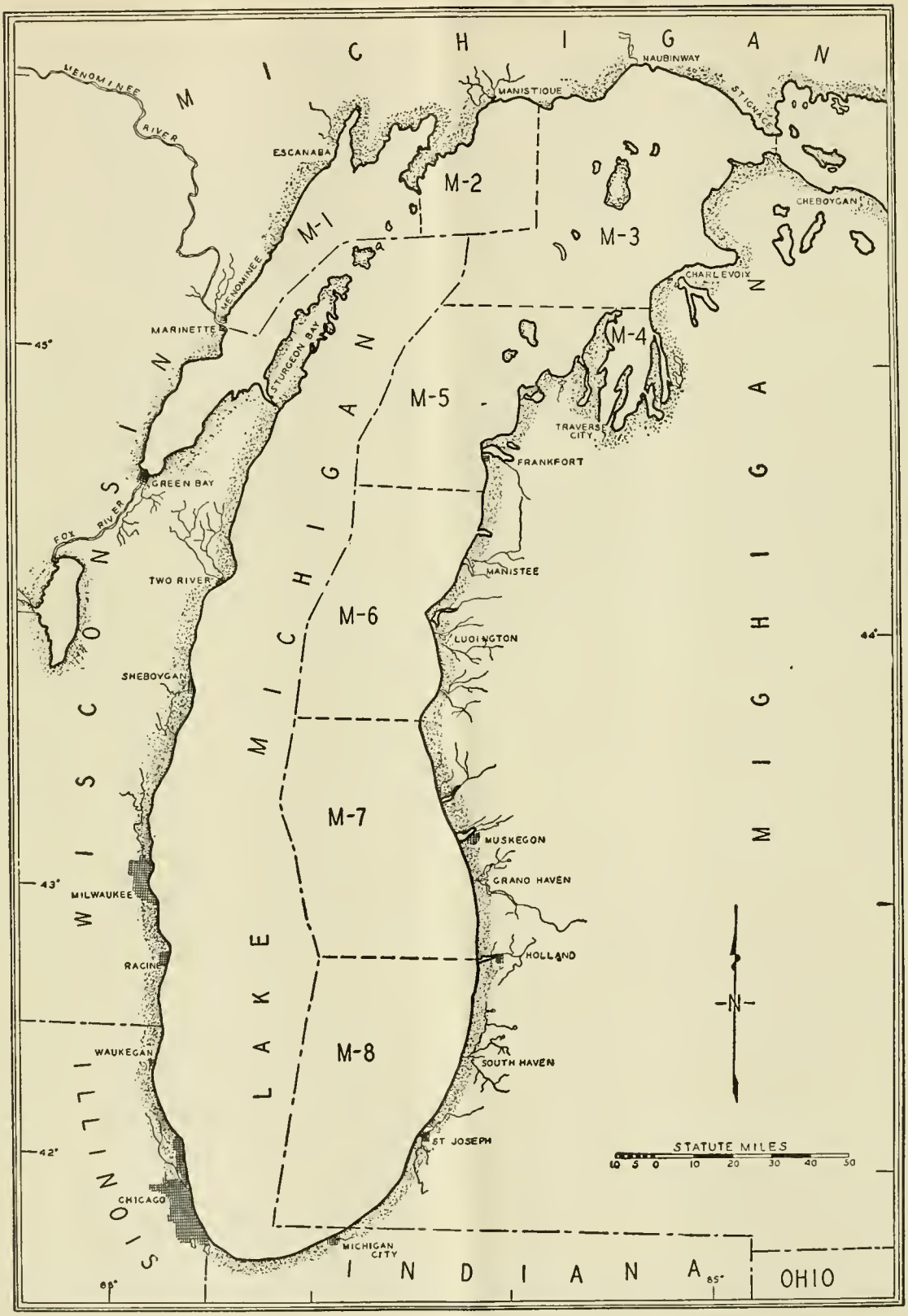

FIGURE 2.—Statistical districts in State of Michigan waters of Lake Michigan.

TABLE 5.—*Comparison of average production of lake trout in Michigan statistical districts, 1891–1908 and 1929–43*

District	1891–1908			1929–43			Change, 1891–1908 to 1929–43, in—		
	Average production [1]	Percentage of total	Rank	Average production [1]	Percentage of total	Rank	Average production [1]	Percentage of total	Rank
M–1	213	6.2	7	146	5.7	7	−67	−0.5	0
M–2	352	10.3	2	266	10.5	5	−86	+.2	−3
M–3	1,500	43.8	1	835	32.9	1	−665	−10.9	0
M–4	108	3.2	8	101	4.0	8	−7	+.8	0
M–5	340	9.9	3	393	15.5	2	+53	+5.6	+1
M–6	297	8.7	5	282	11.1	4	−15	+2.4	+1
M–7	289	8.4	6	224	8.8	6	−65	+.4	0
M–8	325	9.5	4	293	11.5	3	−32	+2.0	+1
Total	3,424	100		2,540	100		−885		

[1] Mean annual production in thousands of pounds.

The large drop in production in M–3 from 1891–1908 to 1929–43 was reflected in a decrease of 10.9 in the percentage contribution of the district to the total output of the State of Michigan waters (from 43.8 to 32.9 percent). The only other district in which the percentage decreased was M–1 (a drop of but 0.5). The remaining six districts experienced increases in percentage that ranged from 0.2 in M–2 to 5.6 in M–5. These changes in the various districts resulted in a noticeable shift of production toward the south. Districts M–1, M–2, and M–3, which, as noted earlier, contributed 60.3 percent of the total in 1891–1908, accounted for only 49.1 percent in 1929–43. The proportion for M–4 through M–8 rose correspondingly from 39.7 to 50.9 percent. A similar shift in production of lake trout toward the south was described for the State of Michigan waters of Lake Huron by Hile (1949).

Rather than burden the present section, which deals with production trends in 1929–49, with numerous unexplained exceptions to general statements, it is believed desirable to anticipate discussion that logically should appear later and describe at this time the peculiar situation in district M–1 that makes the data for that area so difficult to fit into a general account of the lake-trout fishery of the State of Michigan waters of Lake Michigan. This difficulty has its origin in the circumstance that M–1 is not true "lake-trout water" and that the commercial catches of the species are normally part of the production in a fishery aimed primarily at the taking of lake whitefish (*Coregonus clupeaformis*). As a result, the intensity of the fishery for lake trout, and consequently the production as well, are controlled to a large degree by the conditions of the whitefish fishery. This relation is brought out rather forcefully by the data of table 6 on the production, abundance, and fishing intensity for the two species in M–1 over the period 1929–49.

The salient features of table 6 are summarized briefly in the following sentences. First, the production of whitefish in M–1 normally is considerably greater than that of lake trout. In only 2 of the 15 years of the base period 1929–43 was the take of lake trout the greater, and the 15-year average for whitefish was nearly three times that for lake trout. In the years after 1943 the advantage of whitefish was much greater than in the earlier, more nearly normal period. Second, the availability of lake trout and the intensity of the fishery for that species did not exhibit the positive correlation that would be expected if abundance

TABLE 6.—*Comparison of lake-trout and whitefish fisheries in district M–1, 1929–49*

Year	Lake trout			Whitefish		
	Production [1]	Abundance index [2]	Fishing-intensity index [2]	Production [1]	Abundance index [2]	Fishing-intensity index [2 3]
1929	182	71	162	1,140	180	199
1930	203	65	198	1,076	145	238
1931	220	69	204	1,195	143	234
1932	194	80	155	910	120	187
1933	134	97	88	238	66	62
1934	72	92	49	263	91	46
1935	77	87	56	175	89	57
1936	158	137	72	90	75	42
1937	236	157	94	105	65	47
1938	248	112	139	354	104	120
1939	157	94	105	238	86	83
1940	83	105	49	123	74	37
1941	75	138	35	116	90	36
1942	56	96	37	93	80	44
1943	91	100	57	141	92	68
1929–43 mean	146	100	100	417	100	100
1944	47	53	56	232	114	90
1945	29	51	36	234	100	97
1946	11	32	22	514	148	139
1947	46	26	111	2,427	275	397
1948	178	44	253	3,066	221	629
1949	149	45	207	2,263	158	600

[1] In thousands of pounds
[2] Percentage of 1929–43 mean.
[3] Operations with large-mesh gill nets only.

TABLE 7.—*Correlations between abundance and fishing-intensity indices for lake trout and whitefish in district M–1*

Indices correlated	Period [1]		
	1929–41	1929–43	1929–49
Abundance of trout : Fishing intensity for trout	−0.611	−0.553	−0.316
Abundance of whitefish : Fishing intensity for whitefish	.888	.891	.800
Abundance of trout : Abundance of whitefish	−.710	−.690	−.745
Fishing intensity for trout : Fishing intensity for whitefish	.961	.955	.786
Abundance of trout : Fishing intensity for whitefish	−.736	−.704	−.250
Fishing intensity for trout : Abundance of whitefish	.779	.778	.561
Value of r at $p=0.05$	.553	.514	.433
Value of r at $p=0.01$	.684	.641	.549

[1] Data given for two earlier periods as well as for entire 21 years since wartime conditions disrupted normal trends in fishing intensity after 1941 and the extremely low abundance of lake trout introduced a disturbing factor after 1943.

were an important factor in determining the rate of fishing; the correlation that did exist is negative (table 7). It should be emphasized here that the estimate of fishing intensity for a particular species is based only on gear lifted on days when some quantity of that species was captured. Third, the fluctuations in fishing intensity for lake trout followed closely those of the gill-net fishery for whitefish (most lake trout are captured in gill nets), and fishing intensity for whitefish in turn was correlated closely with the fluctuations in the abundance of that species. The data of tables 6 and 7 thus offer rather conclusive evidence that the availability of whitefish is of primary significance in the determination of the intensity of the lake-trout fishery.

The situation just described for district M–1 is not entirely without parallel. Hile (1949) demonstrated that in three districts of Lake Huron in which lake trout and whitefish ordinarily were taken together in a "two-species fishery" (catches of other varieties in this type of fishery are usually unimportant) the fluctuations in the availability of whitefish exerted a readily detectable effect on the fishing intensity for lake trout. The conditions in M–1 merely represent an extreme because of the strongly predominant position of whitefish in the joint fishery and also because of the tremendous upturn in the abundance of whitefish and hence in fishing intensity for both whitefish and lake trout at a time when the availability of the latter species was far below normal.

Comments on the 1929–49 trends of production in the several statistical districts as recorded in table 4 will be based largely on the summary in the top section of table 8. Reference to the production curves of figures 3, 4, and 5 also should prove helpful.

A pronounced difference is to be detected between the "northern" districts (M–1, M–2, M–3) and the remaining or "southern" districts with respect to the calendar years of highest production of lake trout within the period 1929–49. Of

TABLE 8.—*Summary of production, abundance, and fishing intensity for lake trout in Michigan statistical districts, 1929–49*

Item	District								All districts combined
	M–1	M–2	M–3	M–4	M–5	M–6	M–7	M–8	
PRODUCTION:									
3 years of greatest production	1938	1941	1939	1941	1944	1940	1941	1946	1941
	1937	1932	1931	1942	1943	1941	1942	1944	1943
	1931	1931	1930	1944	1941	1932	1932	1945	1940
Last year with production average or greater	[1] 1939	1943	1943	1944	1944	1942	1946	1946	1944
First year of recent progressive decline	[2] 1944	1944	1944	1945	1945	1941	1947	1947	1944
First year with production less than half average	[3] 1944	1946	1947	1947	1947	1947	[4] 1948	1948	1947
ABUNDANCE:									
3 years of greatest abundance	1937	1936	1939	1943	1943	1940	1941	1942	1943
	1941	1933	1941	1935	1944	1941	1942	1943	1941
	1936	1931	1932	1934	1941	1943	1943	1944	1942
Last year with abundance average or greater	1943	1941	1943	1944	1945	1945	1947	1947	1944
First year of recent progressive decline	[5] 1944	[5] 1944	1944	1944	1944	[5] 1944	1942	1943	1944
First year with abundance below 70 percent	[6] 1944	1944	1946	[6] 1947	1948	1949	1949	[6] 1949	1947
FISHING INTENSITY:									
3 years of greatest intensity	(?)	1941	1930	1940	1933	1931	1931	1946	1930
	(?)	1943	1931	1930	1932	1932	1932	1940	1931
	(?)	1942	1938	1932	1937	1930	1930	1935	1932
Last year with intensity average or greater	(?)	1944	1945	1945	1939	1941	1946	1946	1941
First year of recent progressive decline	(?)	1944	1946	1945	1947	1942	1947	1947	[8] 1947
First year with intensity less than half average	(?)	1947	1948	1948	1947	1947	1948	1949	[9] 1949

[1] 1948 and 1949 production above average.
[2] Decline interrupted by increases in 1947 and 1948.
[3] First recent year; production less than half average in 1934 and 1942.
[4] First recent year; production less than half average in 1936.
[5] Decline interrupted by increases in 1948 (followed by further slight rise in 1949 in M–1).
[6] First recent year; abundance below 70-percent level in 1930 and/or 1931.
[7] Fishing intensity so closely linked with availability of whitefish that summary would be meaningless and possibly misleading; see p. 83.
[8] 1941 if irregularities in 1944 and 1946 are ignored.
[9] Intensity unquestionably would have been less than 50 percent of average in 1948 but for the abnormal situation in M–1; see p. 83.

the 9 "high-production" years listed in table 8 for the first three districts, 8 were earlier than 1940 (the 1941 production in M–2 provided the only exception) and 5 earlier than 1935. In districts M–4 through M–8, on the contrary, the highest yields usually came after 1939. Only 2 of the 15 high-production years listed for the southern districts were earlier than 1940 (1932 in M–6 and M–7) and 10 fell within the brief 4-year period 1941–44.

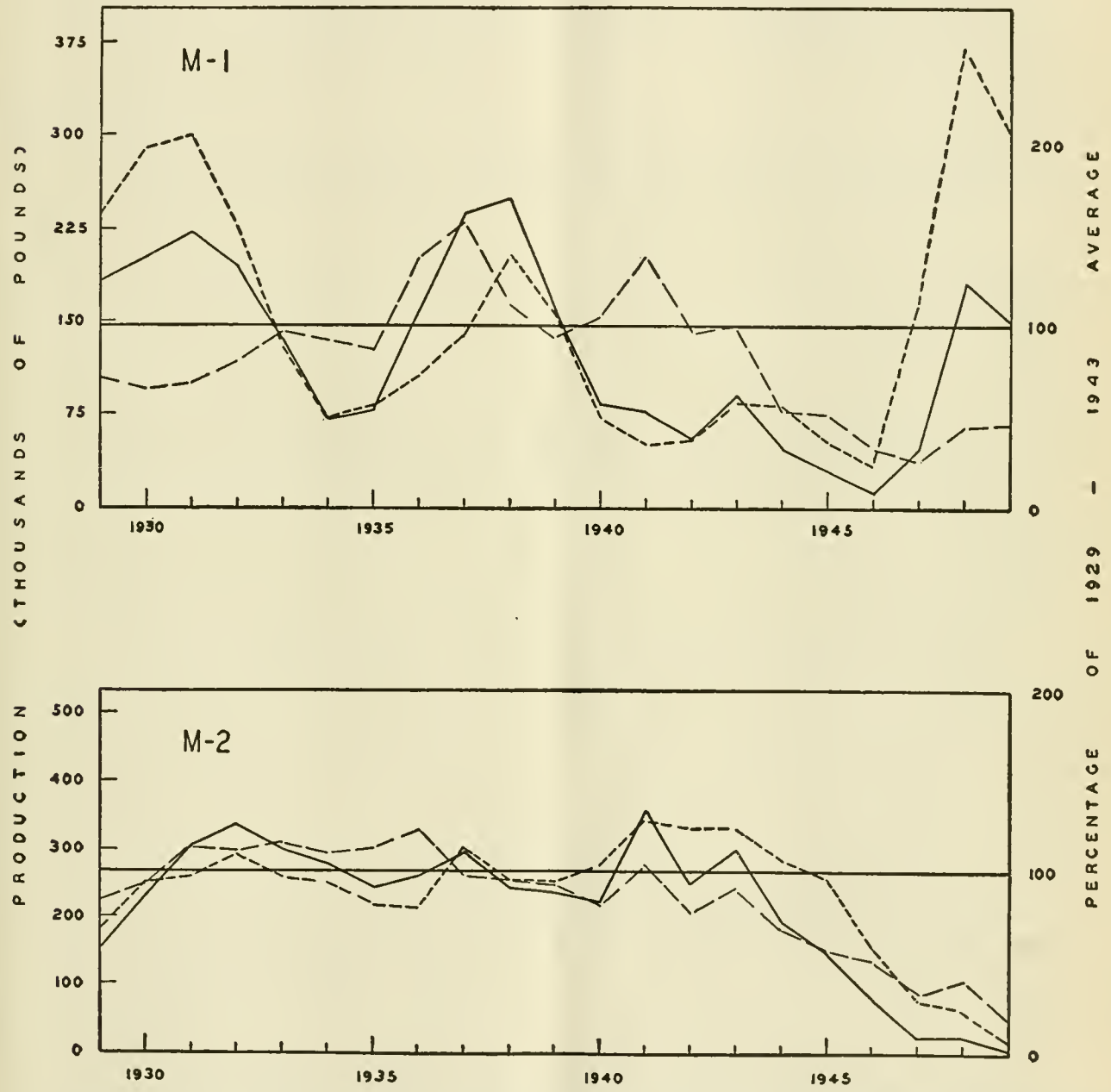

FIGURE 3.—Production, abundance index, and fishing-intensity index for lake trout in districts M-1 and M-2, 1929–49. Solid line = production; long dashes = abundance index; short dashes = fishing-intensity index. Scale at left (thousands of pounds) applies only to production; scale at right is in terms of 1929–43 mean for each item.

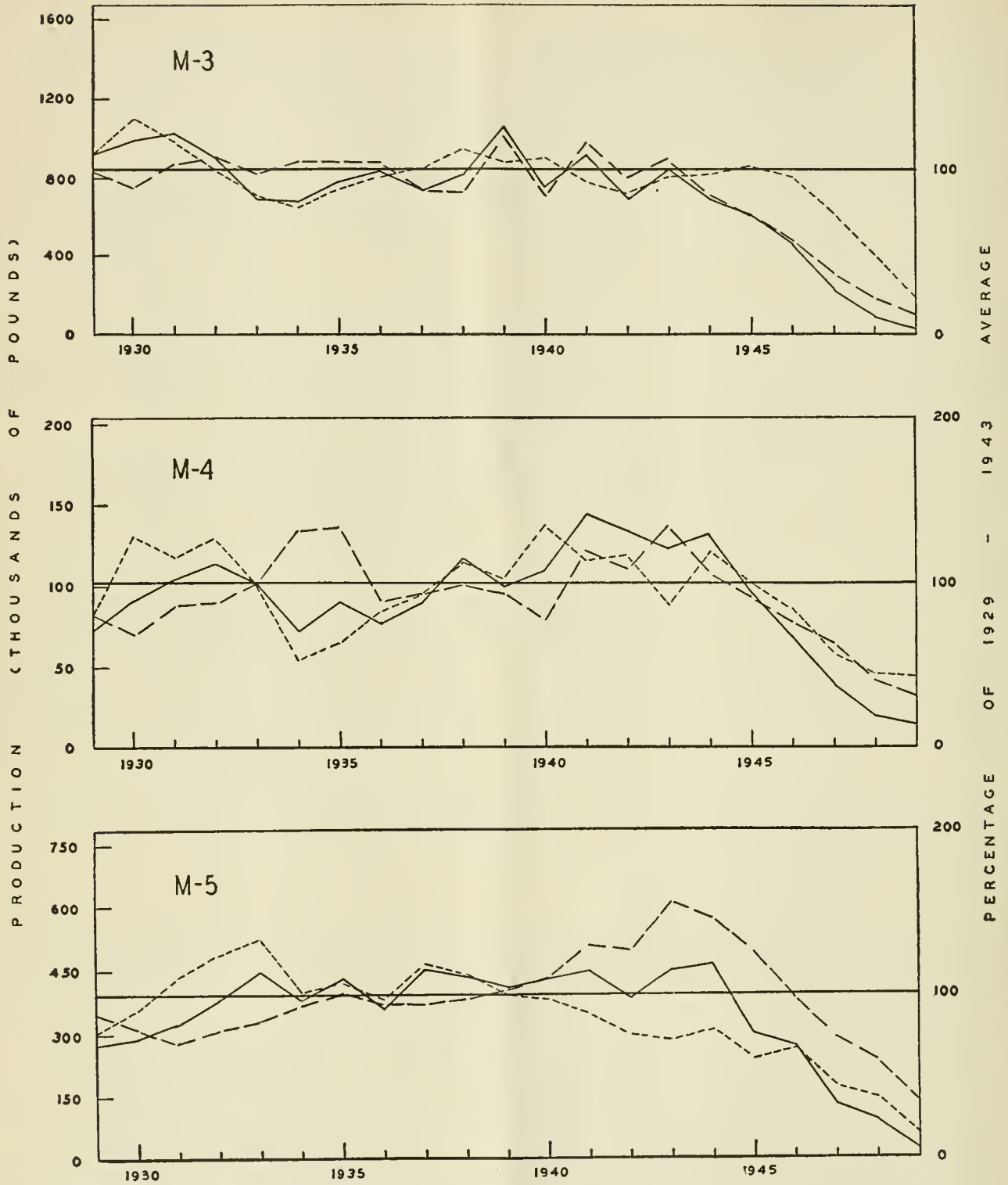

FIGURE 4.—Production, abundance index, and fishing-intensity index for lake trout in districts M–3, M–4, and M–5, 1929–49. Solid line=production; long dashes=abundance index; short dashes=fishing-intensity index. Scale at left (thousands of pounds) applies to production only; scale at right is in terms of 1929–43 mean for each item.

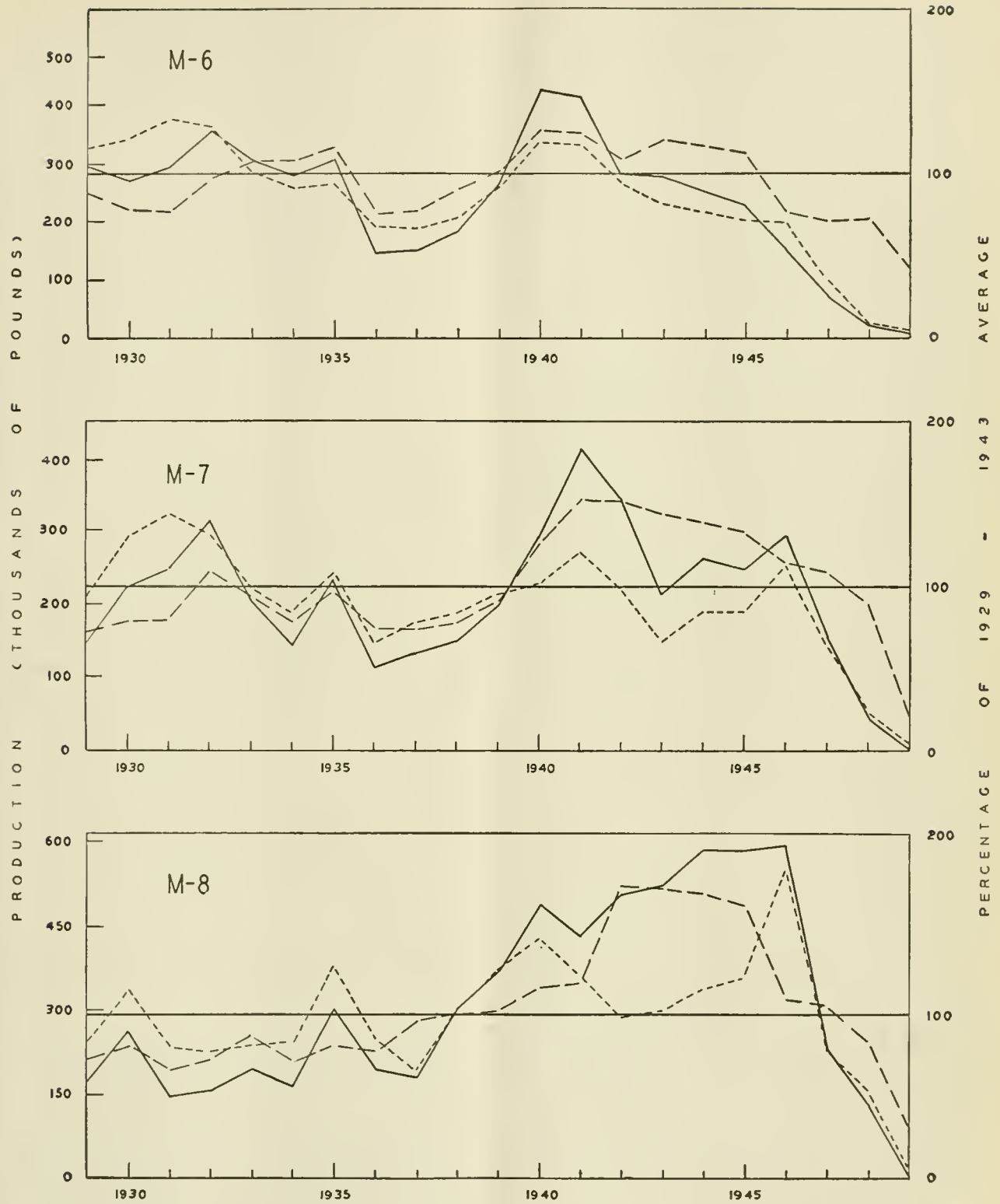

FIGURE 5.—Production, abundance index, and fishing-intensity index for lake trout in districts M–6, M–7, and M–8, 1929–49. Solid line = production; long dashes = abundance index; short dashes = fishing-intensity index. Scale at left (thousands of pounds) applies to production only; scale at right is in terms of 1929–43 mean for each item.

Despite the differences between the northern and southern waters just outlined, all districts agreed in showing production equal to or greater than the 1929–43 mean in relatively recent years. If we ignore the 1948–49 data for M–1, where, as explained, conditions were abnormal, the situation can be described by the statement that every district had average or better production in 1942 or later and in two districts (M–7 and M–8) the take was still above the mean in 1946.

The districts agreed further in that the onset of the progressive decline which has caused so much concern and the drop of production to less than half the average also were recent. In only one of the eight districts (M–6) did the recent progressive decrease get under way before 1944, and in the southernmost waters (M–7 and M–8) it did not start until 1947. With the exception of M–1 and M–2 (again 1948–49 data are ignored in the former district) the 50-percent level was not passed before 1947, and in M–7 and M–8 the take did not drop below half the mean until 1948. These data suggest a distinct north-to-south trend in the time at which the decline set in.

Despite the lateness of the decline, the speed with which it progressed was such that by 1949 the lake-trout fishery had practically come to an end in all districts but M–1. The 1949 total catch for districts M–2 through M–8 was only 74,000 pounds. These same waters had yielded more than 3 million pounds as recently as 1941 and in excess of 2 million pounds as late as 1945. The decline since the latter year represents a decrease of 96.7 percent.

The production data for the combined districts may be summarized as follows: Highest yields occurred in the early 1940's (1941, 1943, 1940); 1944 was the last year of above-average production and the first year of the recent decline; the output fell below 50 percent of the 1929–43 mean for the first time in 1947. Even when data are included for M–1 where the 1949 take was above the 1929–43 average, the decrease from 1944 to 1949 amounted to 90.6 percent.

ABUNDANCE IN STATE OF MICHIGAN WATERS, 1929–49

The estimates of the abundance or availability[7] of lake trout in the statistical districts of the State of Michigan waters of Lake Michigan beginning with 1929 (table 9; see also figs. 3, 4, and 5), are based principally on the records of the catch per unit lift of large-mesh gill nets (mesh sizes 4½ inches and greater, extension measure). During the base period 1929–43, large-mesh gill nets accounted for 88.1 percent of the total catch of lake trout. Set hooks were second (8.2 percent), and pound nets third (2.2 percent). The catch of other gears plus a small quantity of lake trout for which gear records were lacking made up the remaining 1.5 percent (presentation here of original data on gear composition of the catch is not considered necessary). Pound nets were of sufficient importance to be included in the estimation of abundance in only three districts (M–1, M–3, M–4).

Records of the catch per unit of fishing effort of large-mesh gill nets, set hooks, and pound nets in the several districts in 1929–49 are given in tables 10, 11, and 12.

In the listing of the years of highest abundance (middle section of table 8), as was true for the years of greatest production (top section), distinct

TABLE 9.—*Abundance indices for lake trout in Michigan statistical districts, 1929–49*

[Percentages of 1929-43 mean]

Year	Abundance percentage in district—								Average [1]
	M–1	M–2	M–3	M–4	M–5	M–6	M–7	M–8	
1929	71	84	99	80	88	89	72	74	87
1930	65	93	89	69	79	79	79	81	83
1931	69	114	103	86	71	77	79	66	87
1932	80	112	106	88	78	98	110	73	96
1933	97	115	98	100	83	107	94	88	97
1934	92	110	104	132	93	108	79	70	98
1935	87	112	104	134	101	116	96	81	102
1936	137	122	104	89	93	76	75	78	97
1937	157	98	88	92	94	78	74	96	93
1938	112	95	86	99	97	90	78	100	92
1939	94	93	120	93	102	102	91	101	105
1940	105	81	83	77	110	126	126	116	100
1941	138	104	116	119	129	125	153	119	123
1942	96	77	95	108	126	108	151	179	114
1943	100	90	105	134	156	121	143	178	126
1944	53	69	84	105	146	117	139	174	110
1945	51	56	71	91	125	113	132	166	98
1946	32	51	56	76	97	77	115	109	75
1947	26	33	36	63	73	72	108	105	60
1948	44	40	22	40	60	73	89	84	50
1949	45	19	12	30	35	43	21	33	26

[1] In the computation of the averages the abundance index for each district was weighted by the percentage contribution of that district to the total catch of all districts over the 15-year period 1929–43.

[7] Argument about which of the two words should be employed would constitute a futile quibbling over terminology. These estimates are based on the fishing experience of the fishermen—the records of their catch of legal-sized lake trout per standard unit of fishing effort. They offer no information on the abundance of undersized lake trout and are affected by such factors as meteorological conditions, annual differences in the time of spawning in relation to the fixed closed season, and annual differences in the distribution of fish. Yet, for all these obvious weaknesses they offer the best estimates of abundance to be had at the present time. Accordingly, we do not hesitate to use "availability" and "abundance" interchangeably.

TABLE 10.—*Catch of lake trout per lift of large-mesh gill nets in Michigan statistical districts, 1929–49*

[In pounds per lift of 10,000 linear feet of large-mesh gill nets 4½ inches and greater, extension measure]

Year	District							
	M–1	M–2	M–3	M–4	M–5	M–6	M–7	M–8
1929	66	126	131	83	84	98	99	85
1930	57	143	117	66	77	86	111	108
1931	63	175	140	90	72	84	139	92
1932	78	171	143	88	80	107	201	138
1933	106	169	122	88	86	119	140	138
1934	73	168	127	153	96	118	126	91
1935	79	166	136	138	103	127	188	128
1936	168	184	136	97	94	82	148	149
1937	189	146	113	92	95	85	143	163
1938	121	142	113	106	99	98	181	177
1939	96	142	161	101	103	113	189	184
1940	118	121	109	80	113	139	276	212
1941	134	161	155	126	131	137	264	196
1942	91	115	125	118	127	118	247	279
1943	94	136	138	143	158	130	234	260
1929–43 mean	102	151	131	105	101	109	179	160
1944	50	105	109	109	147	129	219	258
1945	48	81	92	92	126	124	212	239
1946	30	78	73	80	98	84	189	158
1947	24	49	47	65	73	79	189	150
1948	42	61	29	42	61	80	143	122
1949	44	28	16	31	35	47	34	48

TABLE 11.—*Catch of lake trout per lift of set hooks in Michigan statistical districts, 1929–49*

[In pounds per lift of 1,000 set hooks. Where no figures are given, few or no lake trout were taken with this gear]

Year	District							
	M–1	M–2	M–3	M–4	M–5	M–6	M–7	M–8
1929	223	173	133	137	356	131	239	252
1930	253	111	143	119	247	108	194	194
1931	201	187	118	123	208	122	132	145
1932	151	218	132	94	138	131	191	116
1933	197	290	229	172	165	72	201	132
1934	247	198	264	139	162	112	154	200
1935	237	259	161	147	202	120	143	162
1936	165	236	182	96	275	------	117	112
1937	154	215	114	191	218	------	122	133
1938	129	207	61	131	433	------	123	140
1939	138	158	111	83	117	------	153	161
1940	129	190	104	143	120	------	134	158
1941	------	91	102	73	------	56	137	176
1942	102	------	------	107	------	------	173	212
1943	------	------	------	------	------	265	249	323
1929–43 mean [1]	184	190	143	128	243	121	164	174
1944	------	------	------	140	------	------	346	73
1945	------	------	------	167	------	------	211	------
1946	------	------	------	------	------	------	185	208
1947	------	------	------	------	------	------	74	435
1948	------	------	------	------	------	------	------	65
1949	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)

[1] For each district for which data are not given for 1 or more years, the 15-year average is estimated by dividing the mean of the available annual averages by the mean of the abundance percentages for the same years. See Van Oosten, Hile, and Jobes (1946) for comments on the estimation of a normal catch when data are not available for all years.

[2] No fishing with set hooks in 1949.

differences are to be seen between the northern and southern areas of the lake. Of the 12 "high-abundance" years listed for districts M–1 through M–4,[8] 9 were earlier than 1940 and only 1 was later than 1941. The corresponding record for districts M–5 through M–8, on the contrary, shows all 12 years within the period 1940–44 and 9 within the still-shorter interval 1941–43.

[8] District M–4, assigned to the southern districts in the grouping with respect to production, has been assigned to the northern with respect to years of greatest abundance.

TABLE 12.—*Catch of lake trout per lift of pound nets in Michigan statistical districts, 1929–49*

[In pounds per lift of 1 pound net. Where no figures are given, few or no lake trout were taken with this gear]

Year	District			Year	District		
	M–1	M–3	M–4		M–1	M–3	M–4
1929	14	17	21	1941	13	12	19
1930	15	16	27	1942	------	8	23
1931	13	15	22	1943	2	12	18
1932	18	16	43				
1933	16	25	47	1929–43 mean [1]	14	15	28
1934	29	17	38				
1935	23	20	66	1944	4	13	9
1936	8	17	24	1945	------	16	------
1937	13	22	33	1946	------	10	10
1938	16	15	17	1947	9	4	2
1939	12	11	13	1948	8	3	7
1940	8	9	16	1949	5	1	------

[1] For each district for which data are not given for 1 or more years, the 15-year average is estimated by dividing the mean of the available annual averages by the mean of the abundance percentages for the same years. See Van Oosten, Hile, and Jobes (1946) for comments on the estimation of a normal catch when data are not available for all years.

Although the recent progressive decline in abundance appears to have started at much the same time in all districts (1942 in M–7, 1943 in M–8, and 1944 in all other districts) it proceeded much more rapidly in northerly than in southerly waters. The last year with abundance at average or greater was 1941 in M–2, 1943 in M–1 and M–3, 1944 in M–4, 1945 in M–5 and M–6, and 1947 in M–7 and M–8. The same north-to-south sequence exists in the first year in which abundance dropped below the 70-percent level,[9] 1944 in M–1 and M–2, 1946 in M–3, 1947 in M–4, 1948 in M–5, and 1949 in M–6, M–7, and M–8. This north-to-south progression resembles closely that described for production in the preceding section. The situation invites speculation about the possibility that a southward spread of the sea lamprey was a contributing factor.

Despite the differences in timing just described, the districts agreed in that all showed an extremely low level of availability of lake trout in 1949 (range of abundance percentages from 45 in M–1 down to 12 in M–3). Admittedly, the dependability of the estimates of abundance decreases rapidly as production falls to low levels. Nevertheless, the consistently low returns per

[9] The 70-percent level is considered preferable here to the 50-percent figure employed for analogous items in the data for production (and for fishing intensity, discussed later). Usually the fishery has all but disappeared by the time the 50-percent level of abundance is reached.

unit of fishing effort together with the very fact that production had all but ended in most areas must be accepted as conclusive evidence of the great scarcity of marketable-sized lake trout in the State of Michigan waters of Lake Michigan in 1949.

For the combined districts the level of abundance was highest in 1943 (126), 1941, and 1942. The last year with abundance above average and the first year of the recent progressive decline was 1944, and abundance first dropped below the 70-percent level in 1947. In 1949 the abundance had reached the low figure of 26 percent.

TABLE 13.—*Correlations between 1929–43 fluctuations in abundance indices for lake trout in Michigan statistical districts*

[Values of r corresponding to probabilities p of 0.05 and 0.01 are ±0.514 and ±0.641]

District	District							
	M-1	M-2	M-3	M-4	M-5	M-6	M-7	M-8
M-1	------	0.113	−0.040	0.175	0.346	0.043	0.142	0.223
M-2	0.113	------	.370	.181	−.460	−.255	−.374	−.617
M-3	−.040	.370	------	.404	.181	.233	.201	−.037
M-4	.175	.181	.404	------	.587	.591	.394	.365
M-5	.346	−.460	.181	.587	------	.681	.786	.889
M-6	.043	−.255	.233	.591	.681	------	.767	.526
M-7	.142	−.374	.201	.394	.786	.767	------	.805
M-8	.223	−.617	−.037	.365	.889	.526	.805	------

From earlier discussion and from the examination of table 9 and figures 3, 4, and 5, it is apparent that in certain districts the annual fluctuations in the abundance of lake trout followed similar trends. In the northern waters for example, it has been pointed out that most of the years of highest abundance fell before 1940, whereas the southern districts shared a period of high availability in the early 1940's. To provide a more precise measurement of the agreement in these trends, coefficients of correlation were computed for the abundance percentages for all pairs of districts over the period 1929–43. Data for years later than 1943 were excluded in order to minimize or possibly eliminate the distorting effects of the decline in abundance that followed the depredations of the sea lamprey in all districts. This restriction, we believe, has made the coefficients recorded in table 13 relatively reliable estimates of the correlations between fluctuations in the availability of lake trout in the different districts under approximately "normal" conditions.

The outstanding feature of the data of table 13 is the close positive correlation among the fluctuations in abundance in the four southern districts (M–5 through M–8). Of the six coefficients that could be computed for these districts, five exceeded the value ordinarily accepted as "highly significant" ($p<0.01$), and the sixth was above the level ordinarily termed "significant" ($p<0.05$). These high values, together with the consistency with which they occurred with all possible pairings, suggest strongly that the lake-trout fisheries to the south of Grand Traverse Point were based on a common stock or on stocks in which the factors controlling abundance in 1929–43 were the same or subject to similar annual fluctuations. Further speculation in the matter would be to little point until we have definite information on the nature of these factors and the methods by which they operate.

The fluctuations of abundance in M–4 exhibited positive significant correlation with those in the two districts immediately to the south (M–5 and M–6). The correlation with fluctuations in M–3 also was positive but the value of the coefficient ($r=0.404$) was well below the level of significance.

Of the 3 coefficients computed between districts M–1, M–2, and M–3, and the 15 calculated between those districts and the ones lying farther south, only one was significant ($r=-0.617$, M–2 and M–8). This single significant value in a group of 18 fails to fit the pattern. The weight of the evidence suggests that the fluctuations in the abundance of lake trout in each of the three northern districts were not correlated with those in the remaining ones.

FISHING INTENSITY IN STATE OF MICHIGAN WATERS, 1929–49

The records of the annual fluctuations in the intensity of the fishery for lake trout (table 14; figs. 3, 4, and 5; bottom section of table 8) fail to reveal the distinct separation with respect to trends that existed between northern and southern areas in production and abundance. With the exception of M–2 where all three years and M–8 where two of the three years of most intensive fishing occurred in the 1940's, the tendency was general for fishing operations to be heaviest in the early 1930's. Of the 21 "high-intensity" years listed in table 8 (see section on production in the

TABLE 14.—*Intensity of fishery for lake trout in Michigan statistical districts, 1929–49*

[In units corresponding to 1/1500 of total expected catch for all districts over 15-year period 1929–43]

Year	District								Tota
	M–1	M–2	M–3	M–4	M–5	M–6	M–7	M–8	
1929	10.1	7.1	35.8	3.4	11.9	12.7	8.3	9.5	98.8
1930	12.3	9.7	42.9	6.2	14.0	13.3	11.5	13.0	121.9
1931	12.7	10.1	38.3	4.7	17.3	14.6	12.7	9.1	119.5
1932	9.6	11.4	32.7	5.2	19.2	14.1	11.5	8.6	112.3
1933	5.4	10.0	27.3	4.1	20.9	11.1	8.9	9.1	96.8
1934	3.1	9.8	25.1	2.2	15.8	10.1	7.5	9.4	83.0
1935	3.4	8.4	28.9	2.6	16.7	10.3	9.5	14.5	94.3
1936	4.6	8.3	30.8	3.3	15.1	7.4	5.8	9.6	84.8
1937	5.8	11.8	32.8	3.8	18.6	7.4	6.9	7.3	94.4
1938	8.6	9.9	36.4	4.6	17.4	7.9	7.4	11.8	104.0
1939	6.5	9.8	33.9	4.2	15.6	10.1	8.4	14.3	102.8
1940	3.1	10.6	34.8	5.5	15.1	13.0	8.9	16.5	107.5
1941	2.1	13.3	30.3	4.6	13.5	12.9	10.6	14.1	101.4
1942	2.3	12.9	28.1	4.8	11.9	10.2	8.8	11.1	90.1
1943	3.6	13.0	31.0	3.6	11.3	8.8	5.8	11.4	88.4
1929–43 mean	6.2	10.4	32.6	4.1	15.6	10.9	8.9	11.3	100
1944	3.5	11.0	31.5	4.9	12.3	8.3	7.3	13.1	91.9
1945	2.2	10.0	32.8	4.1	9.3	7.8	7.3	13.7	87.2
1946	1.4	6.0	31.1	3.5	10.5	7.7	9.9	21.2	91.3
1947	6.9	3.0	23.9	2.4	6.8	3.8	5.6	8.7	61.1
1948	15.7	2.4	15.8	1.8	5.6	1.0	1.9	6.1	50.3
1949	12.8	.7	7.4	1.7	2.4	.4	.4	.7	26.5

various districts for an account of the unusual situation in M–1) 12 fell within the 4-year period 1930–33.

The last year of average or greater fishing intensity was 1939 in M–5, 1941 in M–6, and 1944 to 1946 in the remaining districts. The recent progressive decline started in 1942 in M–6 and in 1944 to 1947 in other areas. Fishing intensity first dropped below the 50-percent level in 1947 in M–2, M–5, and M–6, in 1948 in M–3, M–4, and M–7, and in 1949 in M–8.

For the combined districts the intensity of the lake-trout fishery was greatest in 1930, 1931, and 1932, and the last year of greater-than-average intensity was 1941. The recent progressive decline started in 1947, and in 1949 fishing intensity was only 26 percent of the 1929–43 mean.

The factors that influence the intensity of the fishery for lake trout are so numerous, so variable in their effects, and so difficult to appraise, that in most situations it is impossible to evaluate the effect of any one of them. Among these factors may be listed: Weather conditions; costs of operation; availability of and market for lake trout, for species taken along with lake trout, and for species produced alternatively. During the war years scarcities of equipment and supplies and manpower shortages also affected fishing intensity.

The availability of the lake trout itself well might be expected to exert an important influence on the intensity of fishing since good catches per unit of effort should stimulate fishing operations and poor lifts depress them. This expectation is not borne out, however, by the following tabulation of the coefficients of correlation between the abundance of lake trout and fishing intensity for the species in the various districts in 1929–41:[10]

	r		r
District M–1	−0.611	District M–5	−0.379
District M–2	.034	District M–6	.225
District M–3	−.378	District M–7	.357
District M–4	−.677	District M–8	.633

Of the eight coefficients calculated, four were positive and four negative, and of the three that were "significant" ($r = \pm 0.553$ at the 5-percent level of probability) one was positive and two negative. It is not to be concluded, of course, that a plenitude of lake trout is about equally likely to stimulate or depress fishing activity; rather, it should be stated that in many situations other factors are of greater importance.

The high negative correlation between fishing intensity and abundance of lake trout in M–1 has already been explained. The available statistical data do not suggest an explanation of the even higher negative figure for M–4. Perhaps this significant correlation was merely fortuitous. We are inclined to suspect, however, that the negative correlation can be attributed in part to changes of fishing grounds during the time of the great increase in the popularity of "deep-sea" trolling for lake trout in Grand Traverse Bay (identical with M–4) in the 1930's. Although we have no quantitative measure of the effect on the intensity of the fishery, we do know that certain fishermen, in an attempt to lessen friction between sport and commercial interests, avoided the sport-trolling grounds during the peak of the tourist season and moved their operations to grounds north of Grand Traverse Point (M–3) and near Cathead Point (M–5). Consequently, fishing intensity may have been lower than normally would be expected in some years when lake trout were relatively plentiful.

The significant positive correlation between fishing intensity and the abundance of lake trout in M–8 may reflect a true cause-and-effect rela-

[10] The elimination of years after 1941 in these computations makes possible the best estimate of relations under approximately "normal" conditions since bias from wartime shortages of manpower and materials and the effects of the general sharp decline in abundance that accompanied the increase in the population of sea lampreys in recent years are eliminated or minimized.

tion, but the lack of a similar correlation in the other districts throws some doubt on such an interpretation.

The general situation in the State of Michigan waters seems to be much the same as that in the United States waters of Lake Huron where Hile (1949) concluded that "indispensable as the lake trout may be to the conduct of a lake trout fishery, the abundance of that species is only one of the factors, and in some situations a subordinate factor, in the determination of fishing intensity."

RELATIONS OF PRODUCTION, ABUNDANCE, AND FISHING INTENSITY

Considerable information on the relations of production, abundance, and fishing intensity in the lake-trout fishery of the State of Michigan waters of Lake Michigan was given in the preceding sections. The discussion of the present section is restricted largely to the question of the extent to which production has served as an indicator of fluctuations in the abundance of lake trout and to changes in the fishery immediately preceding and during the recent collapse, with special reference to the possible role of overfishing as a factor in the decline in abundance of lake trout.

The accumulation of information on the degree of reliability of production statistics as indicators of changes in abundance or availability in the Great Lakes fisheries is of importance because in many areas data on the actual take per unit of fishing effort are not available or are at hand for only the more recent years.

The opinion was expressed by Van Oosten, Hile, and Jobes (1946) that "under normal conditions (without disruption in the methods or regulations of the fishery), over limited areas, and for short periods of years, large increases or decreases of production may serve as reliable indicators of increases or decreases in the abundance of fish on the grounds." A similar view was held by Doan (1942) who considered it valid to employ catch statistics for the estimation of the fluctuation in the abundance of several commercially important species in Lake Erie. Doan based his opinion largely on the agreement between trends in the catch of walleyes or yellow pikeperch (*Stizostedion v. vitreum*) per unit effort in the principal gear and the total production of the species in four fishing areas of Lakes Huron and Michigan (data for these two lakes adapted from Hile 1937) and in Lake Erie. More recently, Hile (1949) demonstrated a significant positive correlation between annual fluctuations in the production and abundance of lake trout for four of the six statistical districts of the United States waters of Lake Huron and for the six districts combined. In a fifth area the coefficient was positive with a value corresponding to the 10-percent level of probability, but a significant negative value existed in the sixth district. This negative correlation was explained as the result of the depressing effect of the collapse of the whitefish fishery on the intensity of operations with large-mesh gill nets during years of relatively high abundance of lake trout (note the similar situation described earlier in this paper for district M–1).

Of the coefficients of correlation between the production and abundance computed for Lake Michigan (table 15) those for the period 1929–41 most nearly reflect "normal" conditions. The coefficients for the base period 1929–43 were probably biased by the depressing effects of wartime scarcities of manpower and equipment and those for 1929–49 were affected by wartime conditions and more recently by the general collapse of the lake-trout fishery.

TABLE 15.—*Correlations between production and abundance of lake trout in Michigan statistical districts, for 3 periods*

Item	Period		
	1929–41	1929–43	1929–49
District M–1	−0.050	−0.028	0.337
District M–2	.614	.516	.914
District M–3	.431	.441	.937
District M–4	.065	.223	.712
District M–5	.577	.528	.708
District M–6	.775	.714	.802
District M–7	.904	.817	.802
District M–8	.874	.878	.872
All districts	.579	.596	.918
Value of r at $p=0.10$	.476	.441	.369
Value of r at $p=0.05$	.553	.514	.433
Value of r at $p=0.01$	.684	.641	.549

Actually, the differences between 1929–41 and 1929–43 were unimportant. In both periods the correlations between production and abundance were "highly significant" ($p<0.01$) for M–6, M–7, and M–8 and were "significant" ($0.05>p>0.01$) for M–2 and M–5 and for the combined districts. The positive coefficients for M–3 were moderately high but nevertheless fell short even of the 10-percent value in 1929–41 and barely attained that level in 1929–43. The 1929–41 and 1929–43 data

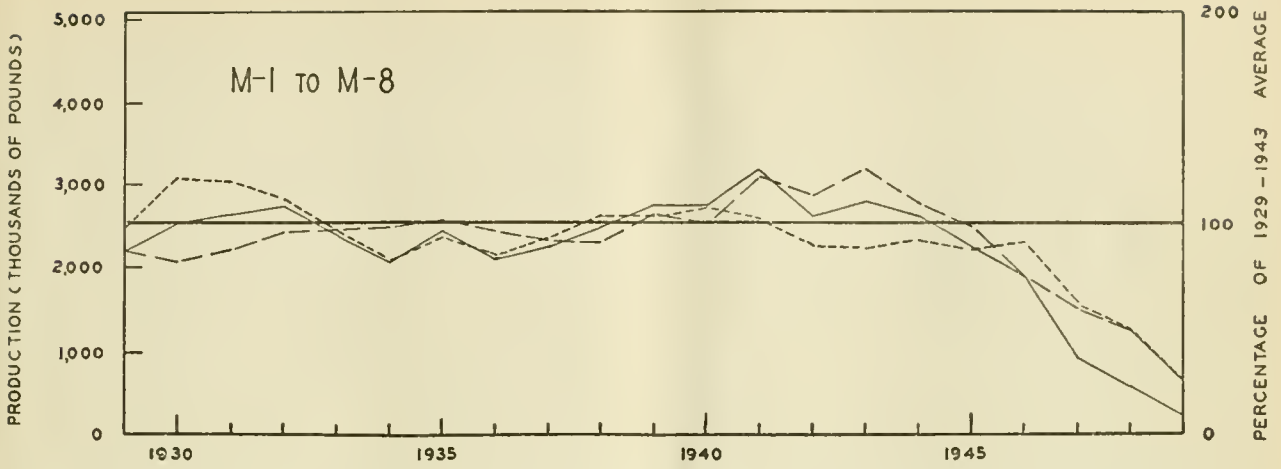

FIGURE 6.—Production, abundance index, and fishing-intensity index for lake trout in combined districts of State of Michigan waters, 1929–49. Solid line=production; long dashes=abundance index; short dashes=fishing-intensity index. Scale at left (thousands of pounds) applies to production only; scale at right is in terms of 1929–43 mean for each item.

offer no evidence for a correlation between the production and abundance of lake trout in M–1 and M–4. A negative correlation between abundance and fishing intensity in each of the two districts in 1929–41 (see preceding section) unquestionably was a major disturbing influence.

From the values of the coefficients for 1929–41 and/or 1929–43 it appears that production served as a more or less reliable indicator of at least the more significant fluctuations of abundance in five of eight districts and in the lake as a whole, was of highly limited value in one district and was completely undependable in two (see figs. 3, 4, 5, and 6). The failure of production and abundance to follow similar courses in M–1 and M–4 (to a considerable extent in M–3 also) brings out the importance of being constantly alert to identify and, if possible, evaluate disturbing factors in the use of production figures for detecting changes in abundance. It should be stressed also that catch statistics should be employed only to detect changes of abundance and not as measures of those changes.

The coefficients of correlation for 1929–49 had high positive values—far beyond the level accepted as highly significant—in districts M–2 through M–8 and in the combined districts. District M–1, where abnormally intensive fishing kept production high in later years, offered the single exception. These high values for districts M–2 through M–8 can be attributed to the enormous declines in both production and abundance that occurred in the later years of the period. Too much should not be made of the high coefficients for 1929–49 as an argument for the value of production statistics for following trends of availability. When a fishery suffers a decline as disastrous as the one that has overtaken the lake-trout fishery of Lake Michigan, statistical analyses are hardly required to prove that fish are too scarce to support commercial operations.

During the years of the decline in the lake-trout fisheries of Lakes Huron and Michigan we heard the opinion expressed both privately and publicly that the sea lamprey had not contributed significantly to the collapse, that the stocks of lake trout simply had dwindled away under the pressure of overfishing, that the distress of the fishing industry was but just retribution for a wanton despoliation of a valuable public resource. The facts given in an earlier study of the lake-trout fishery of Lake Huron (Hile 1949) demonstrated rather conclusively that excessive fishing intensity could not have brought about the collapse of the fishery in the United States waters of that lake. Corresponding data for the State of Michigan portion of Lake Michigan compel a similar conclusion for the lake-trout fishery of those waters.

The data of table 16 (see also fig. 6) fail completely to show a level of fishing intensity that would account for the recent decline in the lake-trout fishery of Lake Michigan. On the contrary, the most intensive fishing operations of the 21-year period, 1929–49, occurred in 1930–32 (112 to 122 percent of the 1929–43 mean—figures that do not indicate excessive fishing even at that time) whereas in the later years fishing intensity has

TABLE 16.—*Indices of production, abundance, and fishing intensity for lake trout in State of Michigan waters, 1929–49*

[Percentages of 1929–43 means]

Year	Production	Abundance	Intensity	Year	Production	Abundance	Intensity
1929	86	87	99	1940	109	100	108
1930	101	83	122	1941	126	123	101
1931	104	87	120	1942	104	114	90
1932	108	96	112	1943	111	126	88
1933	94	97	97	1944	103	110	92
1934	81	98	83	1945	88	98	87
1935	96	102	94	1946	75	75	91
1936	84	97	85	1947	36	60	61
1937	89	93	94	1948	23	50	50
1938	98	92	104	1949	9	26	26
1939	109	105	103				

been invariably below the 100-percent value since 1941. It is particularly significant that intensity was below average in 3 of the 4 years of highest abundance (1941–44) and was barely above the 15-year mean in the fourth. These same years saw production consistently above the mean and at a 21-year peak in 1941, but a high level of abundance, not intensive fishing, was the cause. Furthermore, the intensity percentage exceeded the abundance percentage in only 2 of the 9 years of the period 1941–49; in the remaining 7 years the two index figures were the same or fishing intensity was the lower. It is thus obvious that a rate of fishing that could bring the index of abundance from a record high figure of 126 in 1943 to a record low value of 26 in 1949 simply did not exist. Some factor other than overfishing caused the lake trout to disappear in Lakes Huron and Michigan. The best evidence points to the sea lamprey.

SUMMARY

After a developmental period from 1879 through 1889, the fishery for lake trout, *Salvelinus* [=*Cristivomer*] *namaycush*, in Lake Michigan entered on a 22-year period (1890–1911) of high and relatively stable production. The average annual output for this latter interval was 8,230,000 pounds. There followed two shorter intervals of 15 years (1912–26) and 13 years (1927–39) in which the annual yields were still moderately stable but had successively lower average values of 7,007,000 and 5,293,000 pounds. Production rose in 1940 but the heightened prosperity was short-lived. After 5 years (1940–44) in which the yield was consistently more than 6 million pounds and averaged 6,578,000 pounds, the lake-trout fishery suffered a calamitous decline which saw the annual catch drop from 6,498,000 pounds in 1944 to only 342,000 pounds in 1949.

Michigan and Wisconsin have always contributed the bulk of the production of lake trout in Lake Michigan. The contribution of Michigan for the periods listed in the preceding paragraph (excluding the developmental years for which only scattered data were available) ranged from 42.4 percent in 1890–1911 to 45.7 percent in 1927–39. In Wisconsin the range was from 41.4 percent in 1940–44 to 54.8 percent in 1890–1911. The percentages have been consistently small for Indiana (maximum of 3.1 percent in 1912–26) and were small for Illinois also in the earlier years. More recently Illinois contributed 14.7 percent of the total for the lake in 1940–44 and 11.3 percent in 1945–49.

Comparison of the annual yields of lake trout in the eight statistical districts of the State of Michigan waters of Lake Michigan in 1891–1908 with those of 1929–43 (the base period for our modern statistical analyses) revealed a lower level of productivity in more recent years for every district but M–5 and a slight southward shifting of the centers of production (the northerly districts M–1 through M–3 contributed 60.3 percent of the 1891–1908 total but only 49.1 percent of the 1929–43 yield). The ranking of the districts with respect to their percentage contribution to the lake total changed little, however.

Production statistics for the individual districts in 1929–49 showed that most of the years of relatively high production (the three best years for each district) fell before 1940 in northerly waters (M–1 through M–3) and after 1940 in southerly waters (M–4 through M–8). Although the recent progressive decline in production got under way earlier than 1944 in only one district and started as late as 1947 in M–7 and M–8, the catch had dropped to an insignificantly low level in all districts by 1949 (an exception must be made for M–1 where considerable quantities of lake trout were taken coincidentally in an abnormally intensive fishery for whitefish).

Records of the three years of greatest abundance or availability of lake trout (as computed from the data on the catch per unit of fishing effort of the principal gears) revealed that most of these years fell before 1940 in districts M–1 through M–4, whereas in the waters to the south (M–5 through M–8) they all fell within the period 1940–44. Figures on the last year with abun-

dance at or above the 1929–43 index of 100 and on the first year of abundance below 70 (a level of availability selected as critical in this study) give strong indication of a north-to-south progression in the timing of the recent decline (with the more northerly districts the first to drop below average and to pass the 70-percent level). This sequence suggests that the different areas may have been affected successively as the sea lamprey spread from the north to the south. Despite this progression, all eight districts agreed in exhibiting an extremely low level of abundance in 1949 (from 12 to 45 percent of average in the individual districts; 26 percent for the combined districts).

During the more nearly normal years preceding the recent general decline of the lake-trout fishery, the annual fluctuations in the abundance of lake trout in the four southern districts (M–5 through M–8) were closely correlated. The coefficient of correlation r was highly significant ($p<0.01$) for five of six possible pairings over the period 1929–43 and was significant ($p<0.05$) for the sixth. The fluctuations of abundance in M–4 also were correlated significantly with those in M–5 and M–6. The abundance in each of the northern districts, on the contrary, appeared to be independent of that in any other area.

In the majority of the statistical districts the years of most intensive fishing for lake trout fell in the early 1930's and for the combined districts the three years of greatest fishing intensity were 1930, 1931, and 1932. With the exception of M–1, where a recent upswing in the intensity of fishing for whitefish led to an increased pressure on lake trout, fishing intensity for the latter species entered on a progressive decline as early as 1942 and in no district later than 1947. By 1949, fishing intensity was far below 50 percent of the 1929–43 average in all districts but M–1 and amounted to only 26.5 percent for the eight districts combined. The abundance of lake trout seems to have had little influence on the intensity of the fishery under the normal conditions of 1929–41 (before World War II with its shortages of manpower and equipment and well before the general decline of the lake-trout fishery associated with the spread of the sea lamprey).

During the same normal 1929–41 period, fluctuations in production served as reasonably dependable indicators of major changes in abundance in five of the eight districts. These changes in production did not, however, provide reliable measures of the extent of the fluctuations in abundance.

Statistics on the production and abundance of lake trout and on the intensity of the lake-trout fishery refute the view sometimes advanced that overfishing has been the cause of the decline of the lake trout in the State of Michigan waters of Lake Michigan. The most intensive fishing of the 1929–49 period took place in 1930–32, and intensity has been consistently below the 1929–43 average since 1941. Some factor other than overfishing caused the lake trout to disappear. The best evidence points to the sea lamprey.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

CHARACTERISTICS OF SPAWNING NESTS OF COLUMBIA RIVER SALMON

By Clifford J. Burner

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CONTENTS

	Page
General life history	97
Criteria of a mature redd	97
Measurements and methods	100
Chinook salmon	102
Spring chinook	102
Summer chinook	103
Fall chinook	103
Silver salmon	106
Chum salmon	106
Blueback salmon	107
Redd size and interredd space	107
Summary	110
Literature cited	110

CHARACTERISTICS OF SPAWNING NESTS OF COLUMBIA RIVER SALMON

By CLIFFORD J. BURNER, *Fishery Research Biologist*

Construction of Grand Coulee Dam across the main stem of the Columbia River raised a serious problem concerning the salmon that spawned in the upper reaches of the river and produced an important part of the west-coast catch. Grand Coulee was to be a high dam, with a tailrace-forebay difference of about 350 feet. Although it was possible to provide reasonably safe passage upstream past the dam for the adult salmon, the cost would be extremely high. Of greater importance was the probability that the salmon fingerlings on their way to the sea would be killed in passing down the spillway or through the turbines. It was decided, therefore, to relocate the salmon runs that spawned above the Grand Coulee site in four tributary systems entering the Columbia River below that site. The Wenatchee, Entiat, Methow, and Okanogan Rivers were selected to receive the transplanted salmon.

One of the many questions in connection with the relocation was how many salmon should be placed in each stream or section of stream to get the maximum yield of spawn and fry. To answer this question, a study was made of the spawning habits of four species of Pacific salmon of the genus *Oncorhynchus*. These are the chinook (*O. tschawytscha*), the silver (*O. kisutch*), the chum (*O. keta*), and the blueback (*O. nerka*). This study was concerned particularly with the type of stream bottom that a given species uses for spawning, and the space occupied by a pair of spawning fish for the nest, or redd. The study included redds of salmon spawning naturally in some of the lower Columbia River tributaries and redds of transplanted spawners in the foster rivers. The information obtained was used in planning and carrying out the maintenance project (Fish and Hanavan 1948) but was not published.

At this time, in view of the program for the development of the lower Columbia River tributaries in the interest of salmon production, it seems worth while to set forth the results of the study so that they may be available for reference.

GENERAL LIFE HISTORY

All species of Pacific salmon are anadromous, that is, the adults migrate from the ocean into fresh-water streams to spawn. They proceed up rivers, such as the Columbia, until they arrive at the same tributary where they themselves began life some years before. Very few stray to other streams. The female salmon deposits her eggs in a nest, or redd, which she digs in the gravel of the stream or shallow lake-shore waters. In the process of egg laying, the fertilized ova are covered with successive layers of gravel to a depth of several inches. The time required for the eggs to hatch depends on the temperature of the water. Newly hatched fish live in the gravel of the redd and gradually absorb the food in the abdominal yolk sac. At the end of this period, usually in the late winter or early spring, they struggle up through the gravel and begin to seek food. How long the young fish stay in fresh water varies considerably with the species, but eventually they migrate downstream to the sea, where they remain from 1 to 3 years and grow rapidly. When they approach sexual maturity, they return to fresh water to spawn and thereby complete the cycle. All Pacific salmon die after spawning.

CRITERIA OF A MATURE REDD

At the outset of this study, it was necessary to determine at which stage of development a redd should be measured. Redd building may be divided into three stages, prespawning, spawning, and postspawning. During the prespawning stage, the female salmon is green, that is, the eggs are neither ripe nor loose in the ovaries. Males are seldom in attendance, and are frightened away by the female, who repels all intruders of either sex. The female digs the redd as she turns on either side, at an angle of about 45° to the current, head upstream, body arched, and makes a series of violent flexions with body and tail. (See fig. 1.) The tail strikes the gravel occasionally and the strong-boiling current created carries gravel and

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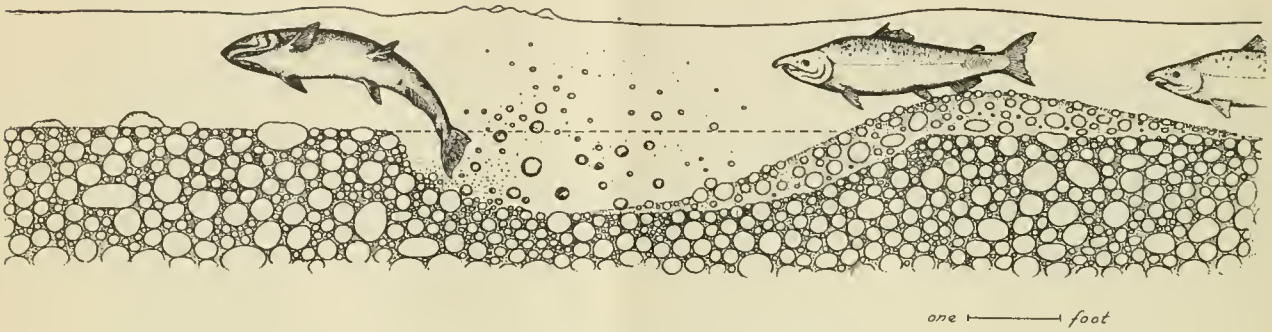


FIGURE 1.—Redd making. Female digging.

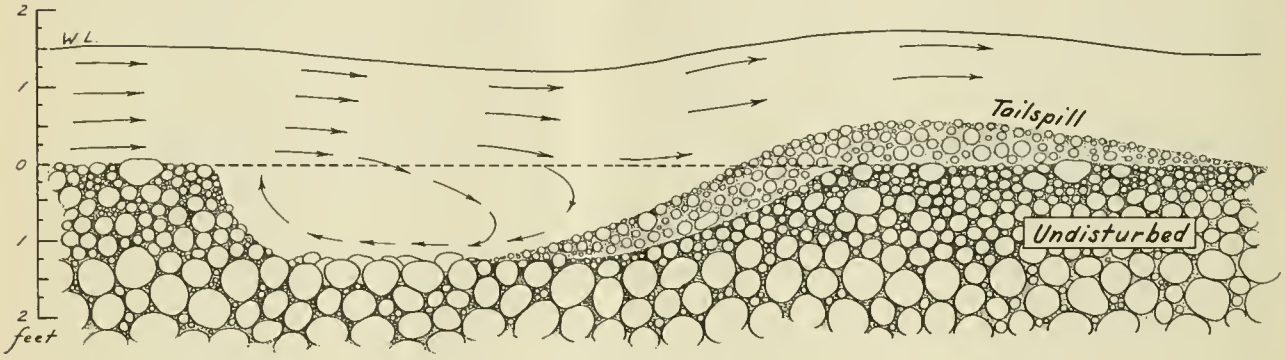


FIGURE 2.—Typical currents in a redd.

silt a short distance downstream. This material spreads out in a flat semicircle at first; then, as the digging upstream proceeds, it collects into a loose pile called the tailspill. With more digging, the redd assumes a long oval shape about twice the length of the salmon and several inches deep. The prespawning digging of the redd may go on for as many as 5 days.

At the beginning of the spawning stage, the nest is ready for the eggs. All loose gravel and fine material have been removed from the pot, or center of the redd, whose shape is such that any current in the bottom flows upstream (see fig. 2), then upward and outward. Usually there remain in the pot large stones too heavy for the fish to move far, and the crevices between these rocks provide excellent lodgment for the eggs. Males are constantly present now. The female alternately digs at the redd and settles back into the depression to release eggs. A male then moves quickly alongside the resting female, as in figure 3, curves his body against hers, and releases sperm in a small milky cloud that settles briefly in the bottom of the redd where the eggs are lodged. The newly deposited eggs are thus surrounded by sperm and eventually fertilized. Excess sperm is carried slightly upstream along the bottom of the redd and gradually carried away by the current. During the spawning stage the redd increases considerably in length and depth, and appears to move upstream as a result of the continued digging at the upstream wall and the filling in of the tailspill area.

The postspawning stage begins after the female

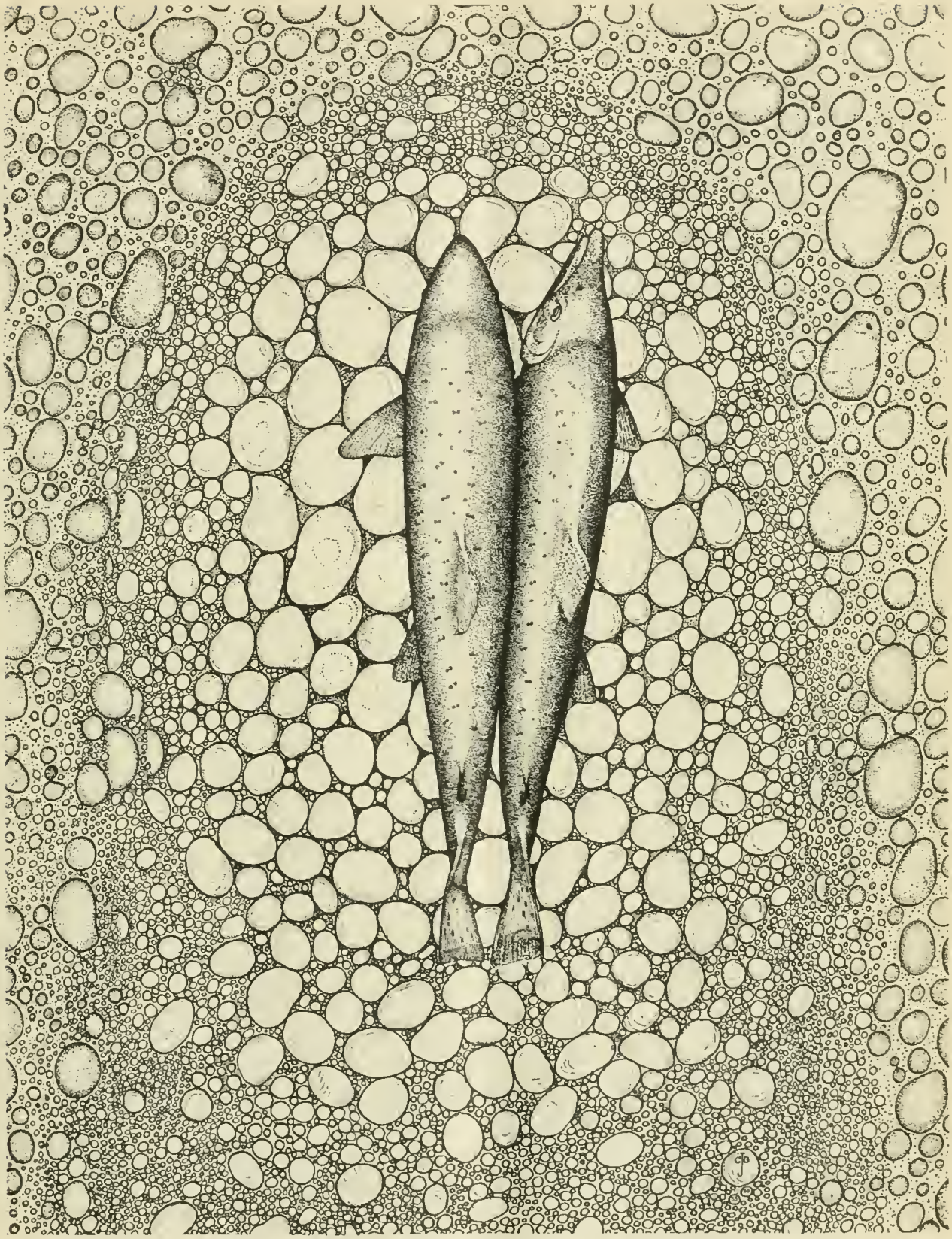


FIGURE 3.—A pair of spawning salmon on a redd.

finishes depositing her eggs. Males are no longer attentive. The female is gaunt and spent, but she continues to dig at the gravel with ever-weakening efforts until she dies. This post-spawning digging, which may continue for 10 days, becomes shallow, off-center, and ineffective. The area of the nest is increased without (after the first day at least) adding to the protection of the eggs.

In view of these facts, a mature redd is considered one in which all egg-laying activities have been concluded, and some postspawning digging has been accomplished.

Several criteria were used to determine whether an observed redd was mature: (1) The gaunt and spent appearance of a lone female salmon still digging—considered the most reliable criterion; (2) the infrequency of the mating act, which becomes sporadic as the supply of eggs is exhausted; and (3) the presence of freshly covered eggs in a redd unoccupied by salmon. Most of the redds measured during the study met the first criterion. For redds observed daily, the second criterion indicated near maturity. Some blueback-salmon redds in which no fish were present were considered mature on the basis of the third criterion.

MEASUREMENTS AND METHODS

Size of the redds was determined by wading into the stream and taking the length, depth, and several width measurements. The outline of the redd was sketched to scale on engineer's notebook paper, with all pronounced irregularities drawn in. Later, in the laboratory, a planimeter was used to compute the area. The entire excavated portion of the redd back to the tailspill's highest point was included in the measurement. The prespawning-digging area, usually located directly under the crown of the tailspill, was thereby included. The long tapering downstream slope of the tailspill was not considered an essential part of the nest measurement, for several reasons: Live eggs were rarely found there; the velocity of the current would carry fine sand and lighter silt considerable distances, resulting in elongation of the slope; and often the downstream slope of the tailspill of one redd would be disrupted by salmon making redds immediately below it. Such tailspill encroachment never proceeded far enough to endanger the eggs laid in the neighboring redd.

Depth measurements were taken from the surface of the water at 1-foot intervals starting at stream bed at the upstream edge of the redd, down the central axis, through the deepest portion, and over the tailspill. A cross section at the greatest depth of the redd was taken in similar fashion from the stream bed on one side to the stream bed on the other.

The gravel composition for each redd was arrived at by estimating the amount of large, medium, and small gravel that had been exposed. The term "large" gravel is used to describe stones more than 6 inches in diameter, but not necessarily round. "Medium" applies to stones from 6 inches down to 3 inches. "Small" applies to those less than 3 inches, but larger than heavy sand.

Stream velocities were taken by clocking a bit of drift over a measured course. The currents and other flow conditions in a redd were determined with an aqueous solution of potassium permanganate.

The times of the salmons' first entry into the streams, the times of first redd digging and of peak of spawning, average stream and redd depths, and water velocities and temperatures are shown in the table.

Except in small, sparsely populated creeks, no attempt was made to measure all the redds in a stream. In rivers thickly covered with redds throughout their length, only representative sections were observed, but all the redds in such sections were measured, in order to avoid selection. In these sections each redd was marked by driving a stake at the downstream slope of the tailspill, or by placing a number on a tree opposite the redd. The stakes facilitated observation, from day to day, of the redd-digging progress of an individual salmon. Figure 4 is a diagram of a redd that was marked on the first day of digging and measured daily thereafter. In this diagram, it will be seen that redd digging extended from September 20 to October 8. The sign of Venus (♀) below the line indicates the female, present each day the redd was measured. The sign of Mars (♂) above the line shows for each day the number of male salmon actively attending and fighting for the privilege of fertilization.

Summary of information gathered on spawning of salmon in selected streams

	Chinook salmon							Silver salmon in Toutle River (1938)	Chum salmon in lower Columbia tributaries [1] (1938)	Blueback salmon			
	Spring run		Summer run			Fall run							
	Ohanapecosh River (1938)	Nason Creek (1939)	Entiat River (1939)	Wenatchee River (1939)	White River (1939)	Kalama River (1938)	Toutle River (1938)			White River (1939)	Little Wenatchee River (1939)	Wenatchee River (1939)	Okanogan River (1939)
Spawning schedule:													
First entered stream	[2]	[2]	[2]	[2]	[2]	Sept. 9	[2]	[2]	[2]	[2]	[2]	[2]	[2]
First redd digging	Aug. 20	Aug. 21	Sept. 7	Sept. 8	Sept. 23	Sept. 20	Sept. 27	[2]	[2]	Oct. 11	Sept. 17	Oct. 2	[2]
Peak of spawning	Aug. 28	Aug. 31	[4]	Sept. 20	[4]	Sept. 30	[4]	Oct. 22	Nov. 22	Oct. 20	Oct. 12	Oct. 8	[2]
Spawning ended	Sept. 10	Sept. 15	Nov. 15	Oct. 25	Oct. 15	[2]	Nov. 2	[2]	[2]	[2]	Nov. 4	Oct. 31	Nov. 15
Depth of stream: [3]													
Average (mean) inches	14	8.6	16	13	10	14	11.6	7.8	10	11.5	12	13	9
Minimum do	2	3	7	4	6	3	3	2	2	3	2	5	4
Maximum do	36	18	26	30	16	48	24	26	30	37	24	28	17
Depth of redds: [3]													
Average (mean) do	9	8.5	10	9.7	9.3	10	10.7	8	8.5	5.5	5.7	4.2	5
Minimum do	3	4	4	4	5	2	4	3	3	3	3	2	2
Maximum do	20	14	19	18	14	17	18	20	17	9	11	8	9
Velocity of water:													
Average (mean) cubic feet a second	[2]	2	1.5	2	1.7	2	1.3	[2]	[2]	1.6	1.7	1.8	1.7
Minimum do	[2]	.5	1	1	1.4	1	1	[2]	[2]	1	1	1.7	1.5
Maximum do	[2]	3.5	2	3	2	3.5	3	[2]	[2]	1.8	1.9	2	2
Temperature (Fahrenheit) of water:													
Minimum degrees	51	47	40	55	47	52	42	42	40	44	48	54	47
Maximum do	53	52	55	62	51	61	58	58	44	49	51	55	48

[1] Germany Creek, Abernethy Creek, Elokomin River, and Grays River.
[2] No data.
[3] Transplanted.
[4] Indefinite.
[5] Average measurements taken from surface to stream bed at each side and at upstream end of each redd.
[6] Depth below stream bed, taken at deepest part of redd.

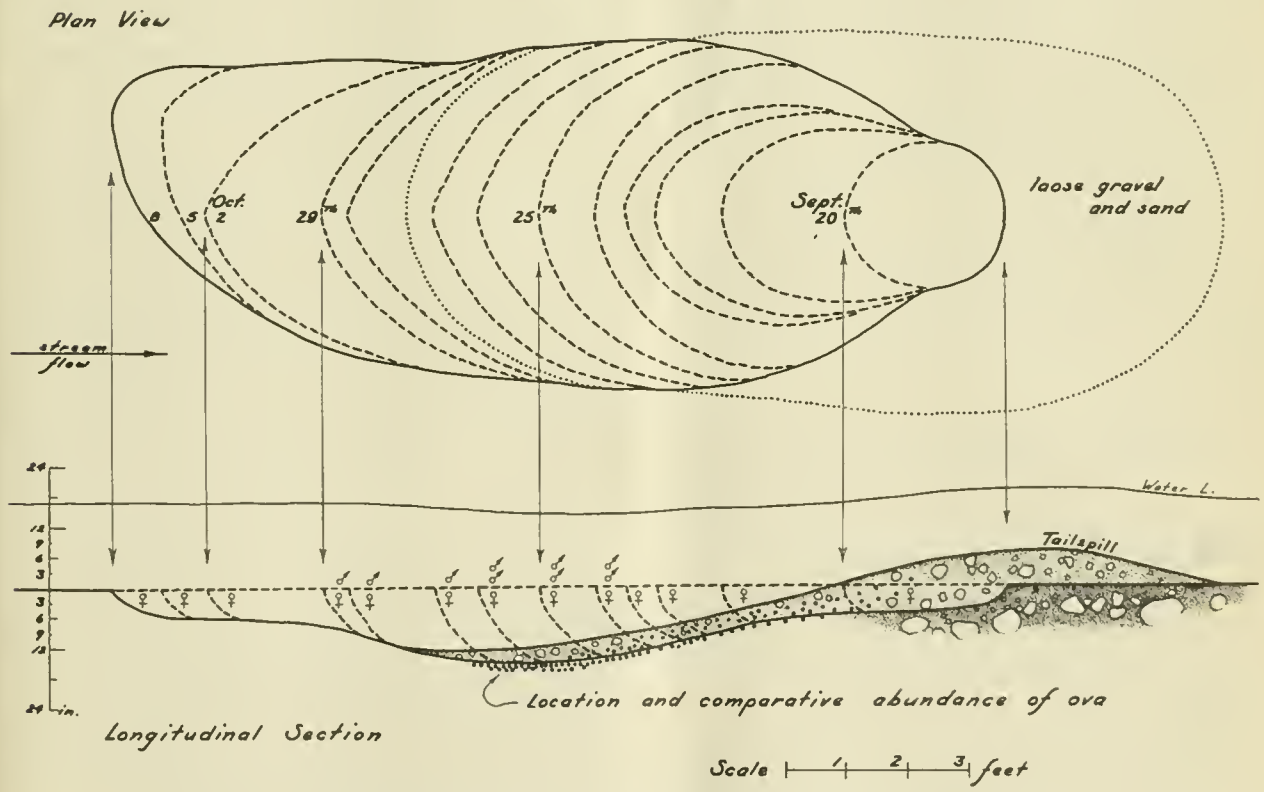


FIGURE 4.—Diagrammatic views of a fall chinook salmon redd measured daily.

CHINOOK SALMON

The chinook salmon is native to the Pacific coast from California to Alaska. Some runs extend from Bering Strait to the southern Siberian coast. By transplantation of fertilized eggs, runs have been established in the St. Lawrence River and in certain parts of New Zealand. The Columbia River supports the largest population of the species.

In the Columbia River, most of the chinook salmon migrate upstream from March through September. The migration is divided into three more or less distinct classes, and the fish are referred to as spring-run, summer-run, and fall-run chinooks, according to the time they leave the ocean and start on their upstream journey. The smaller spring chinooks, which average about 15 pounds in weight, ascend the Columbia River system for considerable distances and spawn in headwaters from mid-July to mid-September. The larger summer chinooks do not go as far upstream as the spring chinooks, and the time of spawning is later, from September to mid-November. The fall chinooks spawn chiefly in the lower Columbia River tributaries and in the main stems of the Columbia and Snake Rivers at about the same time as the summer chinooks, and the two classes are comparable in size. The summer chinooks have an average weight of about 30 pounds, and the fall chinooks average 20 to 25 pounds.

The following three sections describe and compare the size and other characteristics of the redds made by spring, summer, and fall chinook salmon, in several tributaries of the Columbia River.

SPRING CHINOOK

Investigation of spring chinook salmon redds was made in the Ohanapecosh River, a tributary of the Cowlitz River (which is a lower-Columbia tributary), and in Nason Creek, a tributary of the Wenatchee River. The Ohanapecosh has a natural run of spring chinook salmon, whereas the Nason was one of the streams into which fish were transplanted during the Grand Coulee fish-maintenance project.

The average redd size and gravel composition of these two streams may be compared in figure 5*a*, circles A and B. The Ohanapecosh, a mountain stream, contained a high proportion of large rubble about the size of a football. Because of the large-gravel component, the Ohanapecosh redds were considerably smaller (2.9 square yards) than Nason Creek redds (4.9 square yards). The Ohanapecosh redds contained an average of 59 percent medium and small gravel, whereas the Nason Creek redds averaged 86 percent medium and small.

Spawning times, stream depths at the redds, depths of redds, and water velocities and temperatures for the spring-chinook redds in the two streams are given in the table.

SUMMER CHINOOK

The spawning of summer chinook salmon was studied in the Entiat River, the Wenatchee River, and the White River tributary of Wenatchee Lake. These are streams selected as foster rivers for some thousands of the chinook salmon blocked by Grand Coulee Dam. The spawning redds measured were made by the transplanted salmon, trapped at Rock Island Dam near Wenatchee, Wash., in July, August, September, and October. Because of the similarity of summer-run to fall-run chinook salmon in all but time of migration, I have combined the measurements of the summer-chinook redds with those of fall-chinook redds in the size frequency graph, figure 7.

For the 41 redds measured in the Entiat, the average size was 7.8 square yards. A comparison of the Entiat average, figure 5*a*, circle C, with the average nest areas for summer and fall chinooks from other streams shows that the Entiat River redds were distinctly larger than those in other streams. The Entiat River contains an abundance of medium and small rubble which facilitated redd construction and resulted in large redds. The degree of cementation was less in the Entiat than in the Kalama River or the Toutle River (where fall-chinook redds were studied) and probably contributed to the ease of digging. Subsurface percolation was greater, and this is a factor that governs the location of redds to a greater extent than is generally recognized.

It was noted that most spawning took place on gravel through which there was a flow of water. The flow was detected by releasing potassium-permanganate solution in test holes in the stream beds. There were areas in the Entiat River and in nearly all streams examined, apparently unexcelled for redd building and where trial redds were

visible, that were deserted by salmon for no other ascertainable reason than that there was little or no flow of water through the gravel. Gravel firmly cemented with silt and clay binders usually lacked a percolating flow and was avoided by Entiat River chinooks and by salmon in other streams. All species showed a decided preference for moderately bound stream-bed materials in place of either loose shingle (free-rolling gravel) or firmly bound rubble.

Nearly all spawning of summer chinook salmon in the White River took place in areas of the stream that contained 95 percent medium and small gravel. As shown in figure 5*a*, circle D, 9 redds were measured and the average nest area was 4.7 square yards. Although this appears to contradict the inverse-ratio relation between gravel size and redd area, it is not considered significant, in view of the small number of redds measured. As its name implies, the White River is clouded by quantities of chalky glacial material during the summer and fall run-off, and this made observations difficult.

The redds studied in the Entiat, Wenatchee, and White Rivers were made by salmon transplanted to each spawning area over a long period of time. Relocation was spaced out in order to keep the sexes evenly distributed in each area. As a result, there was a mixture of stocks, or races, of summer chinook on the same spawning areas, and a wide assortment of sizes of redds resulted. Although the summer chinook are a little larger, as a class, than the fall chinook, their redds contained about the same proportion of large, medium, and small gravel as fall-chinook redds. Figure 5*a*, circle E, shows that average redd size and gravel composition, for summer chinook in the Wenatchee River are comparable to the redd sizes and gravel compositions for fall chinook in the Toutle River system, figure 5*a*, circles G and H.

FALL CHINOOK

The Kalama River, the Toutle River, and the Green River tributary of the Toutle, were selected for study of fall chinook salmon redds. The Toutle River is a tributary of the lower Columbia through the Cowlitz River; the Cowlitz and the Kalama enter the Columbia only a few miles apart, about 60 miles from the sea. Thus, they are neighboring streams and they have somewhat similar watersheds—both are moderately forested and have fair gradients—but here the resemblance ends. Because of an insurmountable falls, the Kalama River has only 7 miles of available spawning area, containing a high proportion of large gravel. Most of the stream bed is of stratified gravel, that is, stream-bed disturbances and subsequent flooding have overlaid the large gravel with successive layers of smaller stones. During redd digging the salmon encountered the substratum of large rocks with the result that the redds resemble oversize underwater Easter egg baskets. The Kalama River fall-chinook redds contained a higher proportion of large gravel than did other fall-chinook redds. (See fig. 5*a*, circle F.)

The Toutle River and its Green River tributary are both accessible through virtually all their lengths, presenting 40 miles or more of stream bed with a greater choice of spawning rubble than is available to the Kalama River fall chinooks. The areas used contained gravel of relatively uniform size with little or no stratification. Whereas the Kalama River redds averaged 5.7 square yards with 41 percent large gravel, the Toutle River redds averaged 6.5 square yards with 11 percent large gravel.

It would appear, from examination of figure 5*a*, circles F, G, and H, and figure 6, that the abundance of large gravel in the Kalama had the effect of reducing the size of the fall-chinook redds there as compared with fall-chinook redds in the Toutle River and its Green River tributary. The slightly smaller average for the size of the Green River redds, figure 5*a*, circle G, may be attributable to the fact that fewer redds were measured; figure 6 shows that the modal size of the Green River redds is greater than that of the Kalama River redds. These differences might be explained on the basis of the mechanics of redd building: the large gravel in the Kalama was difficult to dislodge and to move, so the resulting redds were smaller, whereas the medium gravel of the Toutle River was easier to dig in and produced larger redds.

SILVER SALMON

Silver salmon are distributed throughout the North Pacific from mid-California to Alaska and in Asiatic waters as far south as Japan. The greatest runs are found in the streams of Oregon, Washington, British Columbia, and southeastern

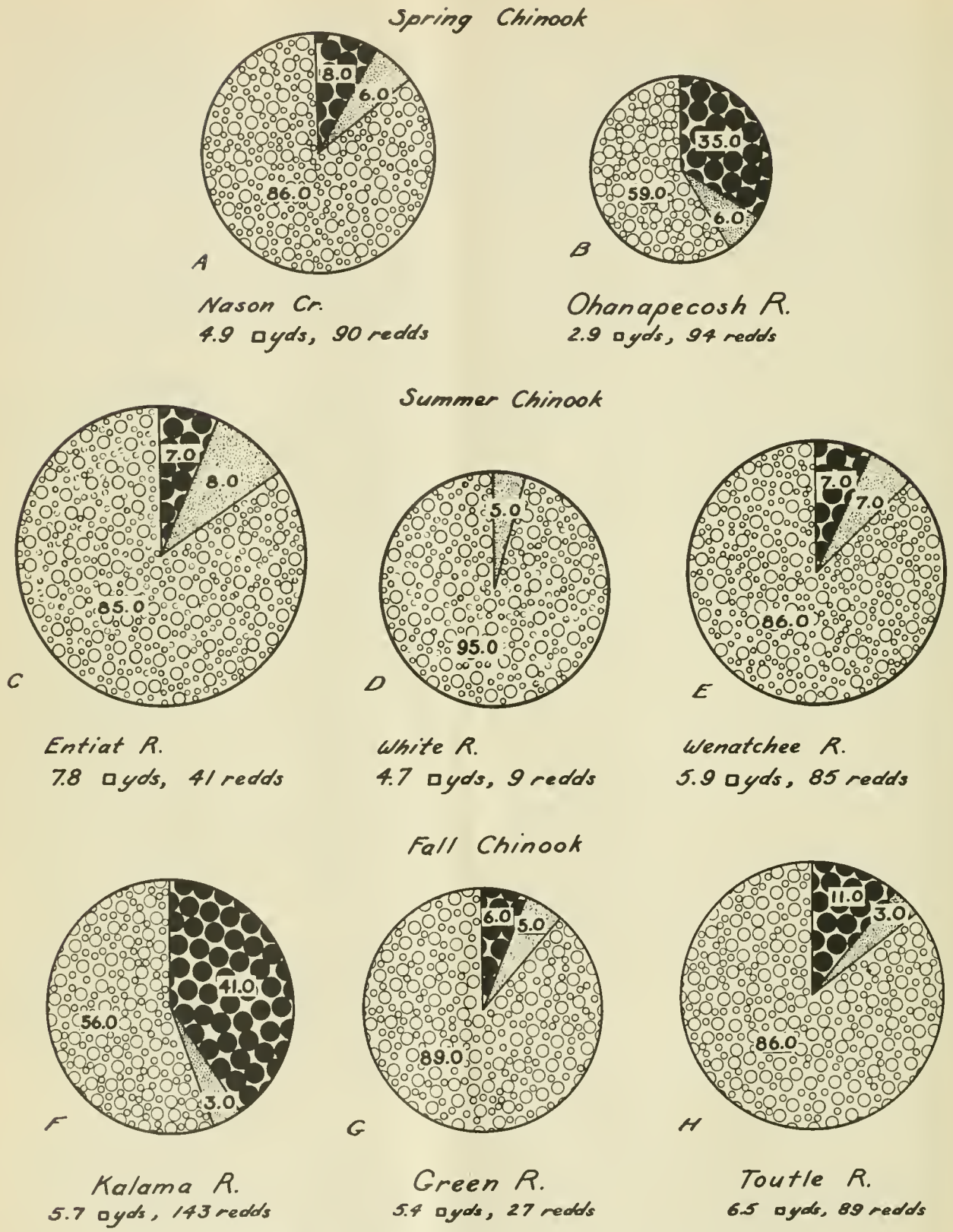
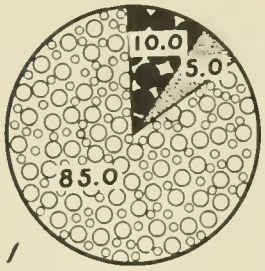


FIGURE 5a.—Average size and gravel composition of Columbia River salmon redds.

Silver

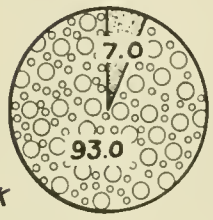


Toutle R.
3.4 □yds, 65 redds

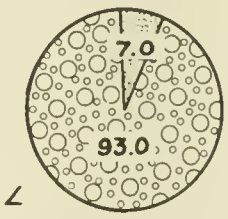
Chum

Lower Columbia tribs.
2.7 □yds, 66 redds

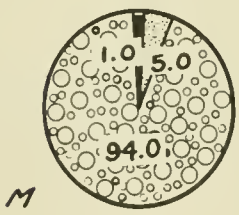
Blueback



White R.
2.0 □yds, 31 redds



Okanogan R.
2.1 □yds, 37 redds



Wenatchee R.
1.8 □yds, 31 redds

Little Wenatchee R.
2.4 □yds, 42 redds

Large gravel - more than 6" diam.
Medium and Small - 6" or less
Mud - Silt - Sand

FIGURE 5b.—Average size and gravel composition of Columbia River salmon redds.

Alaska. At maturity they average about 9½ pounds in weight and about 24 inches in length.

In the upper Toutle and Green River tributaries of the Columbia, the silver salmon occupied many of the same spawning areas as the fall chinooks, and the two species were found spawning at the same time.

In general, the silver salmon apparently prefered small streams flowing only 3 or 4 cubic feet a second and were present in a number of localities not occupied by the chinook salmon. A comparison of the nesting habits of the two species was obtained at a point where the Toutle River is divided by a large bar into a broad and a narrow channel. The small, 3-foot-wide watercourse was populated exclusively by silver salmon. The wider run, nearly 60 feet across, contained only fall-chinook salmon. In the shallower upper reaches of the Green River tributary, the two species spawned virtually side by side.

The silver salmon demonstrated a redd-building versatility that was not equalled by other species. In the small Beaver Creek tributary of the Green River, a stream of less than 2 cubic feet a second, the bottom was composed of flat chunks of slate-shale rubble that defied classification by the usual gravel standards. The silvers were paired off and spawning in stream-width redds that were end to end for a distance of nearly 2 miles. In the Toutle River, immediately below Spirit Lake, silver-salmon redds assumed bizarre shapes, both in surface outline and in bottom contour, as the fish dug around embedded boulders and fallen trees. This was the only salmon of the four species whose redds contained up to 10 percent mud. The gravel composition of silver-salmon redds is shown in figure 5*b* and the size frequency of the redds is shown in figure 7.

CHUM SALMON

Chum salmon are found in rivers of the Pacific coast from Oregon to the Arctic Ocean and in streams of the northern Japanese islands. In the Columbia River these salmon spawn mainly in the small tributaries only a short distance from the sea. They average 26 inches in length and weigh about 10 pounds at maturity.

The streams selected for a study of chum-salmon spawning, Germany Creek, Abernethy Creek, Elokomin River, and Grays River, are tributaries of the lower Columbia River and only a few miles apart. The chum salmon did not migrate far upstream, and in Abernethy Creek some spawned in tidal water so that the redds were uncovered and dry at the surface during a part of each day. Several of the redds were examined when exposed, and live ova were found in the damp gravel of the nest. At high water, these redds were occupied by spawners, but it was not determined whether they were the original occupants.

Chum salmon were also found spawning in water just deep enough to cover the lateral line of the fish. When disturbed they would dash out of the water onto the banks and flop back into the stream. In thickly populated sections, the redds were ill-defined and overlapped from end to end and laterally. The riffles contained hundreds of opaque dead eggs and a few lives ones. Because of the abundance of spawners and the overlapping of nests, it was necessary to select redds for study on the basis of their individuality of outline and apparent maturity. These salmon were more easily frightened than the other species so that it was difficult to determine whether the females were in continuous possession of their redds. In a few instances it was definitely determined that the same females occupied their nests for at least 3 days.

Of 66 chum-salmon redds measured, the average size was 2.7 square yards (fig. 5*b*, circle J). The proportions of large, medium, and small gravel were similar to the proportions for most of the other species. Chum salmon, even more than other species, avoided firmly cemented gravel bottom and spawned in sections of moderately bound rubble where subgravel flow or percolation was evident.

BLUEBACK SALMON

Blueback salmon is the name applied to the species *O. nerka* within the Columbia River System and a few neighboring streams. In Puget Sound and British Columbia they are called sockeye, and in Alaska, red salmon. In the Columbia River, blueback salmon average 3 pounds in weight and 20 inches in length.

The blueback salmon differs from all the other species in that the spawning redds, with few exceptions, are made only in streams tributary to lakes or along lake shores. The young salmon, on emerging from the gravel of the nest, descend

without delay to the lake and live there at least a year before migrating seaward.

Blueback-salmon redds are perfect models of the nests made by larger salmon of other species. The extent of the redd and the size of the gravel chosen are scaled down to the size of the blueback. The number of redds measured, the average size, and the gravel composition are shown in figure 5*b*, circles K, L, M, and N. The gravel composition was 90 percent or more of medium and small size, with the small gravel (about the size of a golf ball) predominating. The stream-type blueback redd contained a small pot of larger stones to receive the eggs, had a loose tailspill, and was oval. The lake-type redd in the shallows near shore in Osoyoos Lake (Okanogan River watershed) was larger and of irregular shape; because there was no current, the female would dig all around the edge of the nest. As there were relatively few of the lake-type redds, none were measured.

REDD SIZE AND INTERREDD SPACE

In general, for all species of salmon the size of the redds varies in direct proportion to the size of the salmon comprising the run, and in inverse proportion to the size and cementation of the gravel in the stream. The redds made in slow water are larger and more circular in outline, but as a rule are not as deep as those made in rapid water where the hydraulic force helps move the gravel.

On crowded spawning gravels of riffles and rapid runs, some chinook redds overlapped slightly end-to-end because the long tailspill of one redd would be disturbed by the female working directly downstream from it. Only a few redds overlapped laterally. As a matter of fact, few redds of any species were made exactly side by side, but occasionally the redds would form diagonal rows across the streams. For the most part, the female chinook salmon was vigorously averse to the presence of another female immediately upstream from her nest, or one digging directly at the side of her nest, until her own redd was well under way.

The natural tendency of the female salmon to guard the privacy of the redd area made for fairly regular spacing. The more or less symmetrical oval shape of most nests was an additional space factor. The salmon redds in a crowded stream area do not fit into each other like the parts of a jigsaw puzzle, but have spaces between them nearly as great as, or greater than, the areas of the nests themselves. This interredd space varies with the species and also with such physical factors as population pressure, composition and gradient of stream bottom, and water velocity. The ratio of interredd space to redd size appeared to be less for chum salmon and silver salmon than for the other species studied. The contiguous and in some cases superimposed construction of chum-salmon redds may have been the result of overpopulation of the limited spawning areas available in the streams examined. Population pressure noticeably decreased the interredd space of silver salmon in Beaver Creek at the upper limit of spawning, where the stream was wide enough for only one or two redds.

In the Kalama River, the large rubble made for smaller redds, but interredd spacing was about the same as elsewhere—presumably because the nest radius to be defended remained the same for chinook salmon of a given size. In quiet-water areas, both redd size and interredd spacing were proportionately greater than the redd size and interredd spacing in stretches of rapid water where the stream bed had considerable gradient. In rapid water, the spawning salmon were busier with redd digging, so that fewer "dog-fights" occurred. Their distribution on the spawning gravels was more or less uniform, resembling the typical spawning-stream population of moderate riffles.

In general it was noted for chinook salmon that, wherever sufficient spawners were present to utilize virtually all the usable gravel, the interredd space amounted to nearly three times the area occupied by the redds. Thus, the total average area necessary for a pair of spawning fish was about four times the area of the average redd. For other species, the space factor was somewhat less than that for chinook salmon. It is believed, however, that to arrive at a conservative figure for the number of pairs of salmon that can satisfactorily utilize a given area of gravel suitable for spawning, the area should be divided by four times the average size of the redds. Thus, a pair of spawning summer or fall chinook salmon would require approximately 24 square yards of suitable gravel; spring chinook salmon, 16 square yards; silver salmon, 14 square yards; chum

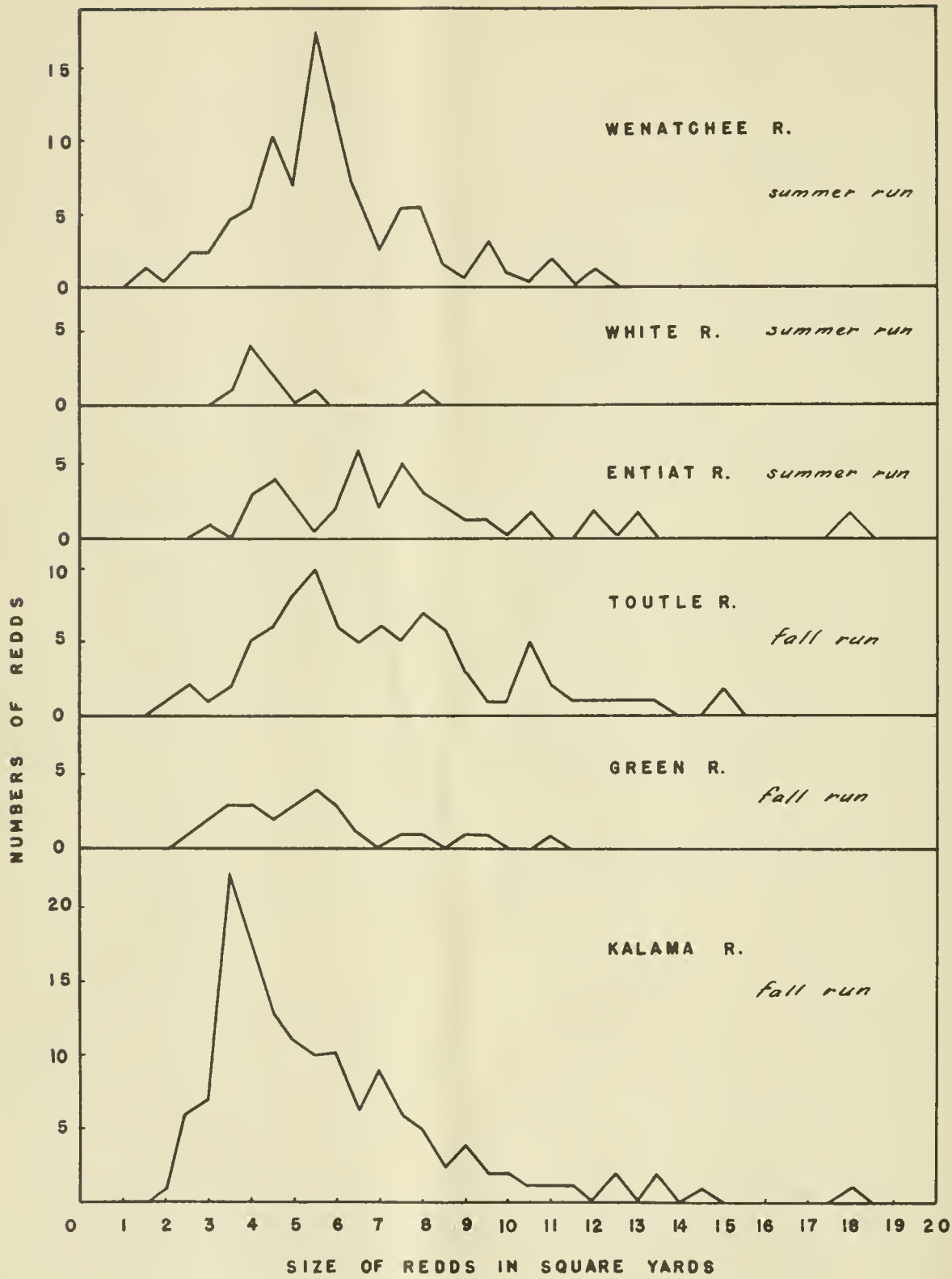


FIGURE 6.—Size frequency distribution of summer and fall chinook redds.

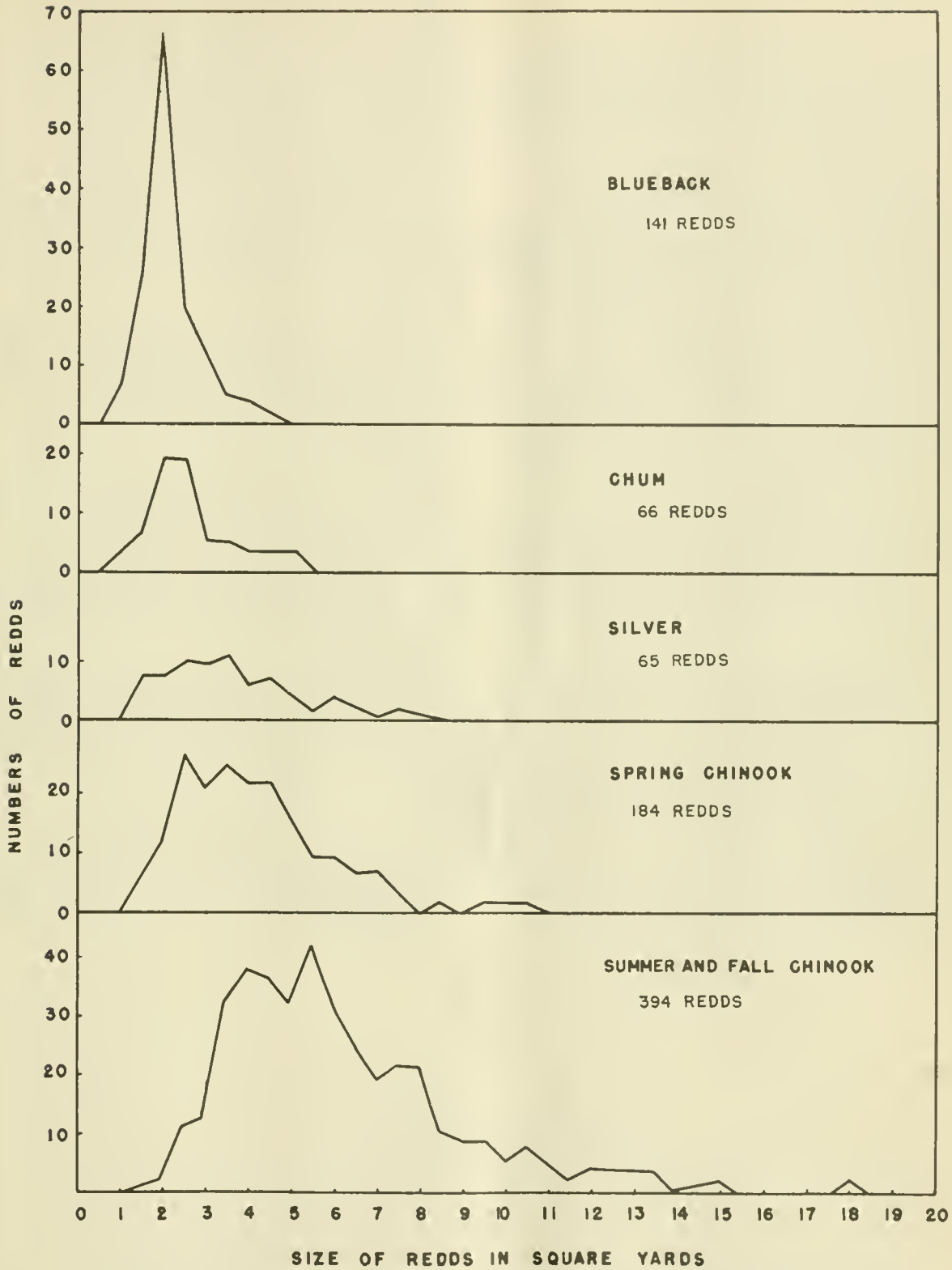


FIGURE 7.—Size frequency distribution of salmon redds from all streams combined.

salmon, 11 square yards; and blueback salmon, 8 square yards.

SUMMARY

1. Observations were made on a large number of chinook, silver, chum, and blueback salmon redds in the Columbia River watershed, and 850 redds were measured.

2. Normally, the female salmon constructs the redd, the male taking no part in this activity.

3. The redd is formed or excavated by the female turning on her side and making violent flexions of the body and tail. The boiling currents set up by this action disturb the gravel of the stream bed which is carried a short distance downstream to form the tailspill.

4. A typical redd is an excavation in the stream bottom, oval in shape, the greatest diameter being lengthwise with the current, and with a tailspill at the downstream end. The center of the redd is referred to as the pot, and it is here that the bulk of the eggs is deposited.

5. Current velocities at spawning areas varied from less than 1 foot a second to 3.5 feet a second. Redds made in fast water were invariably long and narrow; those in quiet water had a broad oval shape.

6. The current in the pot of the redd flows slightly upstream, which favors safe deposition of the eggs in the gravel and is conducive to complete fertilization by the milt of the male salmon.

7. As the spawning progresses, the redd in a sense moves upstream by continued excavation of the upstream edge and filling in of the tailspill area.

8. In general, salmon chose areas of stream bed composed of gravel less than 6 inches in greatest diameter, with the size of the redd inversely proportioned to the size of gravel. Firmly cemented gravel was avoided, though where there was some cementation, the size of the redd was inversely proportioned to the amount of cementation.

9. Percolation of water through the gravel appears to be a requisite of the redd site.

10. In general, salmon prefer areas of stream bottom relatively free of mud or silt for redd-making purposes. Silvers (*O. kisutch*) were the only salmon of the four species which constructed redds in areas of stream bottom containing up to 10 percent mud.

11. Average redd size for the various salmon is as follows: Summer and fall chinook, 6.1 square yards; spring chinook, 3.9 square yards; silver, 3.4 square yards; chum, 2.7 square yards, and blueback, 2.1 square yards.

12. Few redds of any species were made side by side. For the most part, nests were either up or down stream from each other so that they would form diagonal rows across the stream.

13. The tendency of female salmon to prevent other females from getting too close resulted in interredd space approximately three times the size of the redd.

14. By dividing the area suitable for spawning in a given stream by four times the average redd area, a conservative estimate will be obtained of the number of salmon that may satisfactorily spawn in the stream.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

CONTRIBUTIONS TO THE BIOLOGY OF TUNAS FROM THE WESTERN EQUATORIAL PACIFIC

By Bell M. Shimada

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CONTENTS

	Page
Collection of data	111
Notes on tuna spawning	113
Yellowfin (*Neothunnus macropterus*)	113
Big-eyed tuna (*Parathunnus sibi*)	114
Records of juvenile oceanic skipjack (*Katsuwonus pelamis*)	116
Occurrence of bluefin tuna (*Thunnus orientalis*)	117
Summary	118
Literature cited	118

CONTRIBUTIONS TO THE BIOLOGY OF TUNAS FROM THE WESTERN EQUATORIAL PACIFIC

By BELL M. SHIMADA, *Fishery Research Biologist*

Research into the biology of Pacific tunas has advanced rapidly in recent years, yet much remains unknown about the life history and habits of tuna species inhabiting waters of the former Mandated Islands now known as the Pacific Trust Territories, in the western equatorial Pacific Ocean. In prewar years, some scientific studies were conducted by the Japanese, but these were limited in scope and directed primarily towards exploitation of the extensive tuna resources to be found near their island possessions.

With the opening of the Trust Territories on May 11, 1950, to Japanese mothership-type tuna-fishing operations, an opportunity was given the Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service to gather important data on tunas of this region by sending a scientific and technical observer along with the first mothership expedition to leave Japan. I was subsequently detailed aboard the mothership *Tenyo Maru No. 2* and accompanied the expedition from June 12 to September 14, 1950. During this assignment my principal duties were to observe Japanese methods of fishing and processing tuna, and to collect morphometric data on various tuna species for use by the Pacific Oceanic Fishery Investigations in current studies on Pacific tuna populations. Some information was obtained also on other biological aspects of tunas. These incidental observations on the spawning of yellowfin and big-eyed tuna, on the occurrence of juvenile oceanic skipjack, and on the capture of adult bluefin tuna in the area covered by the expedition are summarized in this report.

These studies were made possible through the cooperation of the High Commissioner for the Trust Territories of the Pacific Islands and the Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers. The assistance rendered by various members of the Japanese Fishery Agency and the Taiyo Fishing Co., Ltd., aboard the mothership is also acknowledged.

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COLLECTION OF DATA

The expedition, consisting of a mothership and 25 longline-fishing vessels, commenced its activities in the vicinity of 4°35′ north latitude and 143°32′ east longitude on June 17, 1950. As the season progressed, the center of fishing gradually shifted eastward at a rate of about 100 nautical miles a week, the changes in position of the vessels being dictated largely by the success of fishing in any one area. The deployment of fishing vessels in a north-and-south direction was bounded by 1° and 9° north latitude, but in general fishing was mostly between 1° and 5° north latitude, for it was here that the best catches were made. When operations were terminated on September 5, 1950, the mothership's position was 8° north latitude, 153°46′ east longitude, whence it returned to Japan. The easternmost limit reached by the catcher boats was 160° east longitude. In all, the expedition fished an area of approximately 305,000 square miles from which it took over 4,055 tons of tunas, spearfishes, sharks, and other fishes (table 1).

TABLE 1.—*Total catch, by species, of Japanese tuna mothership expedition, June–September 1950*

Species	Catch [1]
	Pounds
Yellowfin tuna (*Neothunnus macropterus*)	4,574,358
Big-eyed tuna (*Parathunnus sibi*)	699,014
Albacore (*Thunnus germo*)	65,378
Bluefin tuna (*Thunnus orientalis*)	3,430
Skipjack (*Katsuwonus pelamis*)	6,968
Black marlin (*Makaira mazara*)	1,760,389
White marlin (*Makaira marlina*)	48,182
Striped marlin (*Makaira mitsukurii*)	1,229
Sailfish [2] (*Istiophorus orientalis*)	28,160
Swordfish (*Xiphias gladius*)	13,656
Shark	895,022
Others [3]	23,048
Total	8,118,834

[1] Statistics provided by the Japanese Fishery Agency and converted to pounds using conversion factor of 8.27 lbs.=1 *kan*.
[2] Includes short-nosed marlin (*Tetrapturus brevirostris*).
[3] Includes barracuda (*Sphyraena argentea*), wahoo (*Acanthocybium salandri*), and dolphin (*Coryphaena hippurus*).

A few tunas were caught by pole and line at the surface, but gear employed chiefly was the longline. This type of gear was developed to a great

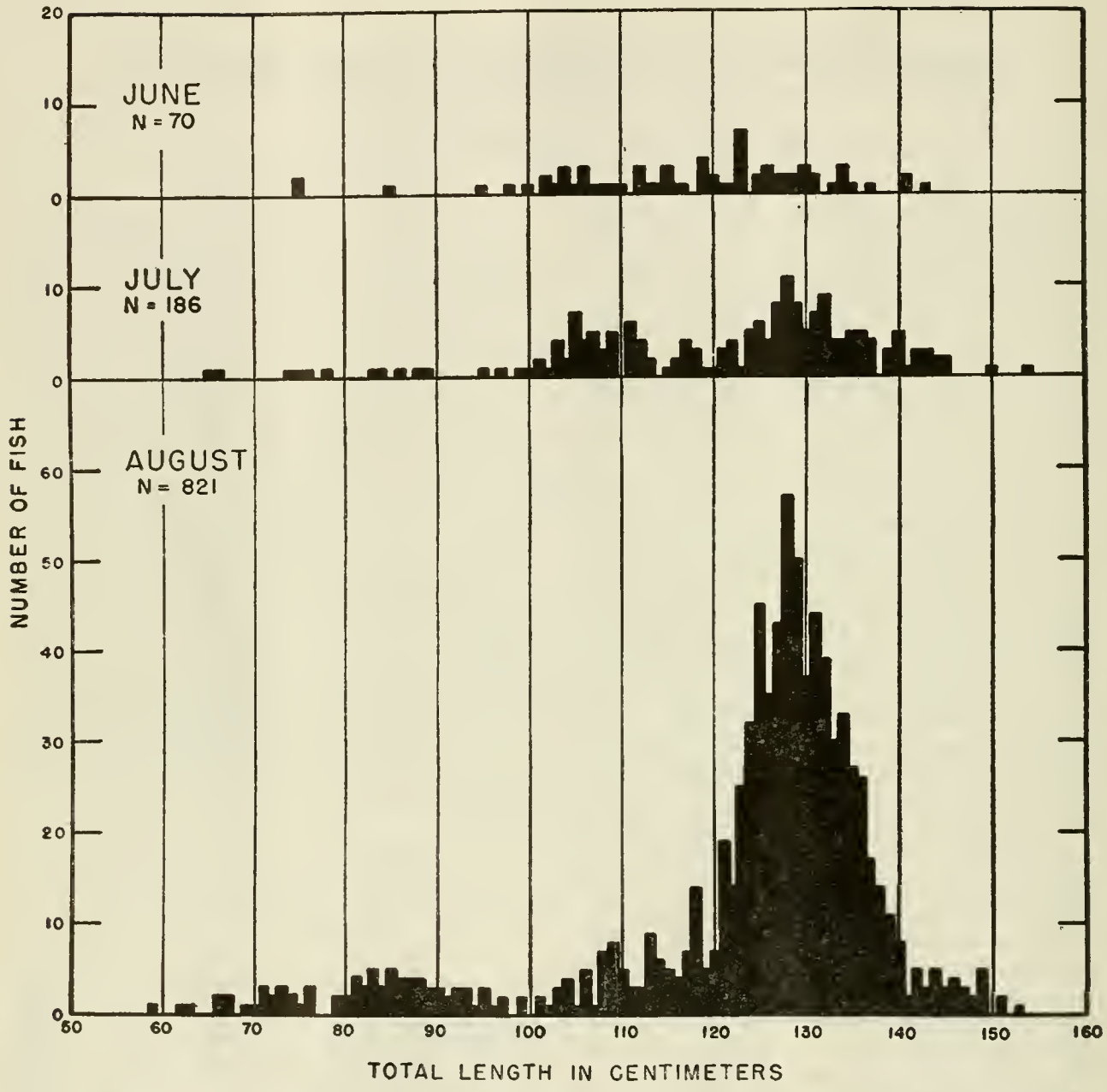

FIGURE 1.—Length frequencies of yellowfin tuna measured aboard the mothership *Tenyo Maru No. 2*, June–August 1950.

extent by the Japanese and is highly effective for fishing subsurface levels for tunas and other commercially valuable fishes otherwise unavailable to fishermen. Although variations in the construction of gear and minor differences in operating technique existed among the many fishing vessels of the expedition, the longlines were built and handled essentially in the same manner by all vessels. A good description of Japanese longline gear and fishing methods is given by Shapiro (1950).

The principal species of fish landed was the yellowfin tuna (*Neothunnus macropterus*) which comprised more than 50 percent of the total catch by weight and number. Yellowfin tuna, because of their export value, were delivered to the mothership as whole fish for freezing, whereas other species were usually gutted at sea. Those yellow-

fin not suitable for freezing in the round because of size or condition were butchered for filleting. Such fish were examined whenever possible for sexual maturity and food habits.

The big-eyed tuna (*Parathunnus sibi*) appeared less frequently in the catches than yellowfin tuna but ranked second in percentage composition of tuna landings by weight and number. Approximately 350 tons of this species were received by the mothership. Biological observations were made on big-eyed tuna similar to those for the yellowfin.

NOTES ON TUNA SPAWNING

Yellowfin (*Neothunnus macropterus*)

Previous studies on the gonads of yellowfin tuna have been largely confined to smaller fish, less than a meter in length, usually captured by surface-trolling gear (Schaefer and Marr 1948a, Wade 1950a). Schaefer and Marr's work (1948a) on the spawning of yellowfin tuna in Central American waters included large fish, but even so, representative samples from catches made by bait boats and purse seiners were composed predominately of fish measuring less than a meter. It is apparent, therefore, that fishing gear designed to fish at or near the surface catches smaller and younger fish than subsurface gear and for this reason does not supply material that gives information on the maturation of older fish.

The longline, on the other hand, captures larger fish. This is evident from figure 1 which shows the plotted length-frequency data for yellowfin tuna taken randomly from longline catches during the season. Length frequencies of fish of less than 80 cm. include not only those caught by longlines but also fish taken at the surface by pole-and-line gear.

Although the proportion of males was usually greater than that of females among yellowfin tuna examined, the sex ratio sometimes running as high as 80 males to 20 females in samples drawn from landed catches, no effort was made to analyze the condition of male gonads for it is extremely difficult, if not impossible, to make a reliable estimate of the state of maturity by gross examination. Milt was found in the central lumen of practically all testes examined, even in those which, from all appearances, would be classified either as spent or as ripening.

Female yellowfin tuna occurred more frequently among fish below 130 cm. in length than among the larger size groups, but in no case was it observed that the proportion of females exceeded that of males.

Ovaries of the fish examined were found to be immature, ripening, or in spent condition, by Marr's criteria (Schaefer and Marr, 1948a) of gonad classification. Since the yellowfin tuna probably spawns several batches of eggs over an extended period of time, as suggested by Schaefer and Marr (1948a), the ovaries possibly do not immediately become much reduced in size after spawning. A long-extended spawning season, with individuals spawning more than once, would result in an ovary ripening over a long period. For these reasons, it is difficult, as others have found, to distinguish between spawning and ripening ovaries. The tabulated results of gonad observations, table 2, probably include both of these categories under the classification of "ripening."

No ovaries that could be considered ripe or running ripe were found. The absence from catches of individuals ready to spawn has been noted wherever studies have been made on the spawning habits of yellowfin tuna. Schaefer and Marr (1948a) observed no running ripe females and hypothesized that, as spawning approaches, the fish either migrate beyond the range of the fishery or stop feeding. In the Philippine Islands, Wade (1950a) found ripe yellowfin in the course of his investigations but no spawning or spent individuals. Apparently this phenomenon is not limited to the yellowfin tuna, for it has been observed for big-eyed tuna (*Parathunnus sibi*), as noted later, and for oceanic skipjack (*Katsuwonus pelamis*) (Hatai et al. 1941).

During early August, yellowfin females with spent ovaries started to appear among catches made 150 to 200 miles east and northeast of Kapingamarangi Island (1°05′ N., 154°45′ E.). Some such ovaries, flabby in appearance and dark red in color, might also have been observed in late July if a check had been made then of incoming fish. Spent ovaries were observed up to the time fishing operations ceased in September.

From these superficial observations of gonads, it was conjectured that the yellowfin tuna to the east of Kapingamarangi Island had spawned in

TABLE 2.—*Sexual maturity of female yellowfin tuna caught in the western equatorial Pacific, June–August 1950*

Date examined	Approximate date of capture	Approximate locality of capture		Total length	Sexual maturity
		Latitude	Longitude		
				Millimeters	
June 25	June 22	3°20′ N.	141°53′ E.	1,269	Ripening.
Do	do	3°20′ N.	141°53′ E.	1,285	Do.
Do	do	3°20′ N.	141°53′ E.	1,269	Do.
Do	do	3°20′ N.	141°53′ E.	1,379	Do.
Do	do	3°20′ N.	141°53′ E.	1,416	Do.
Do	do	3°20′ N.	141°53′ E.	1,230	Do.
June 26	do	2°51′ N.	142°07′ E.	1,485	Do.
June 30	June 26	2°25′ N.	143°27′ E.	1,427	Do.
July 2	June 27	1°51′ N.	145°43′ E.	1,294	Do.
July 6	July 2	2°06′ N.	145°46′ E.	1,324	Do.
Do	do	2°06′ N.	145°46′ E.	857	Immature (or spent?)
Do	do	2°06′ N.	145°46′ E.	884	Do.
Do	do	2°05′ N.	142°10′ E.	1,142	Ripening.
Do	do	2°05′ N.	142°10′ E.	1,413	Do.
Do	do	2°05′ N.	142°10′ E.	1,189	Do.
Do	do	2°05′ N.	142°10′ E.	1,144	Do.
Do	do	2°05′ N.	142°10′ E.	1,064	Do.
Do	do	2°05′ N.	142°10′ E.	1,255	Do.
Do	do	2°05′ N.	142°10′ E.	1,032	Do.
Do	do	2°05′ N.	142°10′ E.	1,120	Do.
Do	do	2°05′ N.	142°10′ E.	1,232	Do.
Do	do	2°05′ N.	142°10′ E.	1,243	Do.
July 8	July 3	1°37′ N.	144°05′ E.	1,189	Do.
Do	do	1°37′ N.	144°05′ E.	1,446	Do.
Do	do	1°37′ N.	144°05′ E.	893	Do.
July 9	July 5	2°12′ N.	149°25′ E.	1,418	Do.
Do	do	2°12′ N.	149°25′ E.	1,353	Do.
Do	do	2°12′ N.	149°25′ E.	1,347	Do.
Do	do	2°12′ N.	149°25′ E.	1,257	Do.
Do	do	2°12′ N.	149°25′ E.	1,181	Do.
Do	do	2°12′ N.	149°25′ E.	638	Immature.
Do	do	2°12′ N.	149°25′ E.	673	Do.
Do	do	1°49′ N.	149°08′ E.	1,367	Ripening.
Do	do	1°49′ N.	149°08′ E.	1,222	Do.
Do	do	1°49′ N.	149°08′ E.	1,249	Do.
Do	do	1°49′ N.	149°08′ E.	1,364	Do.
Do	do	1°49′ N.	149°08′ E.	1,281	Do.
Do	do	1°49′ N.	149°08′ E.	1,303	Do.
Do	do	1°49′ N.	149°08′ E.	1,256	Do.
Do	do	1°49′ N.	149°08′ E.	1,344	Do.
July 13	July 9	4°25′ N.	150°58′ E.	1,420	Do.
Do	do	4°25′ N.	150°58′ E.	1,408	Do.
Aug. 3	July 29	1°18′ N.	155°30′ E.	1,428	Do.
Do	do	1°18′ N.	155°30′ E.	1,390	Do.
Do	do	1°18′ N.	155°30′ E.	1,154	Do.
Do	do	1°18′ N.	155°30′ E.	1,203	Do.
Do	do	1°18′ N.	155°30′ E.	1,350	Do.
Do	do	1°18′ N.	155°30′ E.	1,279	Do.
Do	do	1°18′ N.	155°30′ E.	1,233	Spent.
Do	do	1°18′ N.	155°30′ E.	857	Immature (or spent?).
Do	do	1°18′ N.	155°30′ E.	881	Do.
Do	do	1°18′ N.	155°30′ E.	1,212	Spent.
Do	do	1°18′ N.	155°30′ E.	1,471	Ripening.
Do	do	1°18′ N.	155°30′ E.	1,315	Do.
Do	do	1°18′ N.	155°30′ E.	1,312	Do.
Do	do	1°18′ N.	155°30′ E.	1,343	Do.
Aug. 4	July 31	1°10′ N.	157°29′ E.	1,395	Do.
Do	do	1°10′ N.	157°29′ E.	1,498	Do.
Do	do	1°10′ N.	157°29′ E.	1,213	Do.
Do	do	1°10′ N.	157°29′ E.	1,465	Spent.
Do	do	1°10′ N.	157°29′ E.	1,365	Do.
Do	do	1°10′ N.	157°29′ E.	1,307	Ripening.
Do	do	1°10′ N.	157°29′ E.	1,277	Do.
Aug. 20	Aug. 15	3°35′ N.	155°45′ E.	1,302	Do.
Do	do	3°35′ N.	155°45′ E.	1,275	Do.
Aug. 29	Aug. 26	2°22′ N.	156°34′ E.	1,092	Spent.
Do	do	2°22′ N.	156°34′ E.	1,250	Do.

NOTE.—Y. Yabuta of the Nankai Fisheries Experiment Station, Tokyo, Japan, assisted in making part of these observations.

July with active spawning commencing in June and extending into August. Further hypothesizing that a common yellowfin population had been fished during the season—and there appears to be no evidence to the contrary—it does not seem unreasonable to believe that spawning had occurred coincidentally throughout the area fished. The spawning season is most likely a long one and may not necessarily be limited to the summer months, but the peak of spawning probably is attained during that period.

Yellowfin tuna found elsewhere in the tropical western Pacific Ocean are generally believed to spawn most actively during the summer months. Preliminary studies by biologists of the Pacific Oceanic Fishery Investigations indicate that during 1950 this species spawned in the vicinity of the Hawaiian Islands from early June to September. In the eastern Pacific, however, the spawning season is considered to be during the late winter and early spring months (Schaefer and Marr 1948a). This variation in time of spawning may be connected to some extent with latitude, or it may be a race-connected characteristic. Differences in spawning times of different races of the same species in the same or similar places have been observed in other species of fish, such as the Pacific surf smelt (Schaefer 1936) and European herring (Lissner 1934).

Big-eyed tuna (*Parathunnus sibi*)

Since big-eyed tuna were usually eviscerated at sea, as previously mentioned, I was not able to examine many reproductive organs of this species. No check was made of the maturity of male fish, but some females that were brought in whole were opened and examined throughout the fishing season from late June to early September. These females possessed either ripening or ripe ovaries, with a few having what could be considered advanced-ripe ovaries. No running-ripe or fully spent ovaries were found. Ovaries classified as ripening may have been in a spawning state, because the big-eyed tuna, like the yellowfin, probably spawns over an extended period with successive batches of eggs being ripened and extruded.

Ovaries that appeared ripe were greatly enlarged, round in cross section, and light pink in color. Those approaching the running-ripe stage had translucent ova which were ready to emerge from the follicles. A sample of 1,000 eggs from such an ovary removed from a 1,102-mm. female showed a modal group of large eggs centering around 1.06 mm. in diameter (fig. 2). The largest eggs measured approximately 1.22 mm. The eggs probably increase a little more in size as water is absorbed after emission into the sea.

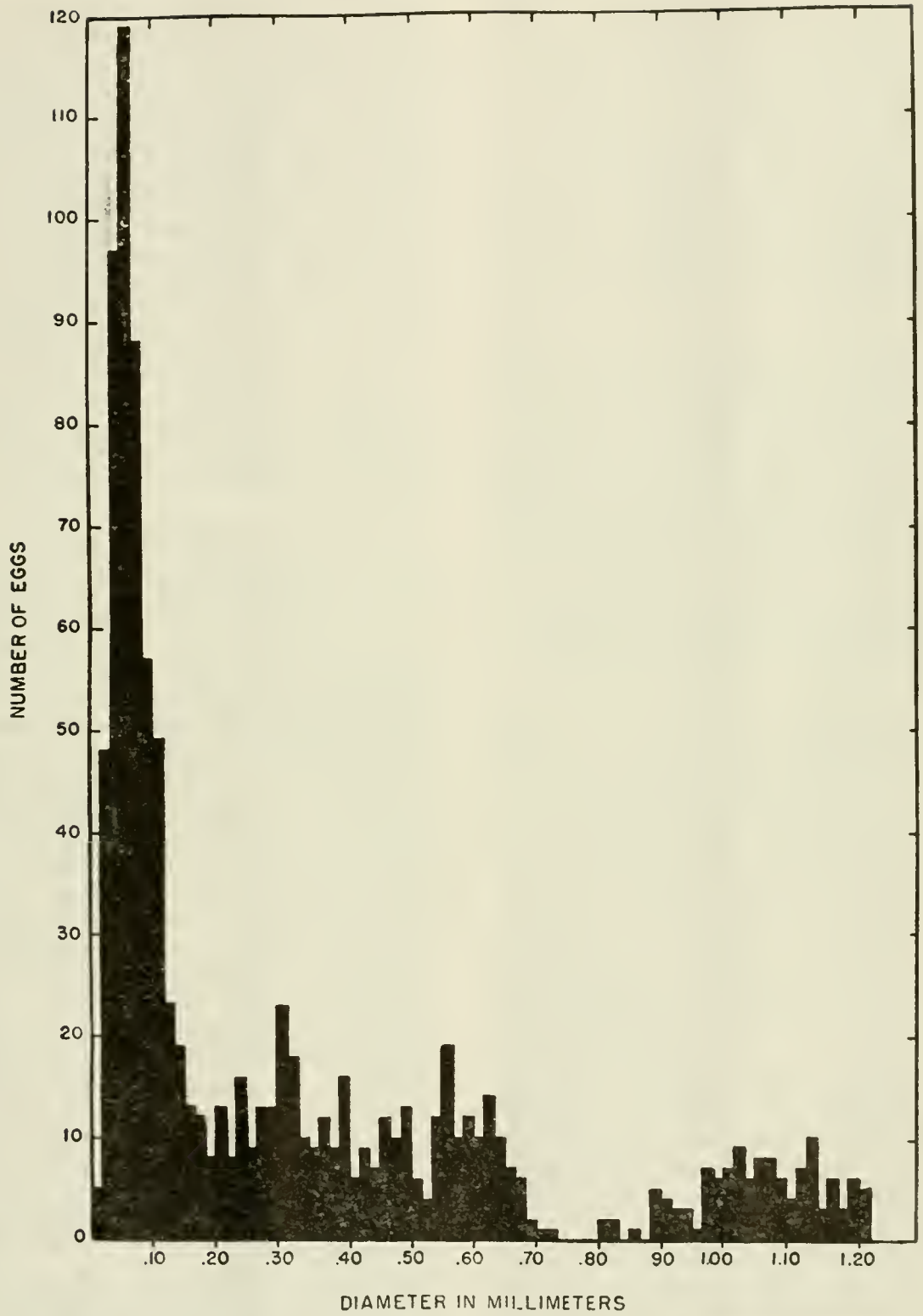

FIGURE 2.—Frequency histogram of ova diameters for a sample of 1,000 *Parathunnus sibi* eggs.

From these observations of gonads it may be inferred that the big-eyed tuna also spawns in the area south of the Caroline Islands. Partial verification of the existence of spawning grounds in these waters is furnished by Marukawa (Hatai et al. 1941), who reported at a gathering of Japanese scientists convened to discuss tuna and skipjack spawning that "Juveniles of big-eyed tuna measuring 4.2 to 4.3 inches were found inside yellowfin tuna taken by longlines in the Tokobei area (Tobi Island, 3° N., 131°31′ E.) last year, while I was in Palau, by a ship of the Fisheries Experiment Station." No mention is made, however, of the date of capture. Despite careful search, juveniles of big-eyed tuna were not found in the many stomachs of yellowfin tuna and other pelagic fishes examined aboard the mothership.

Little is known of the spawning season of the big-eyed tuna; observations, however, suggest that it spawns from June to September, and possibly later. The possibility is not excluded that spawning may be a year-round phenomenon.

RECORDS OF JUVENILE OCEANIC SKIPJACK (*KATSUWONUS PELAMIS*)

While examining stomachs of fish landed aboard the mothership, I recovered and preserved in formalin seven juvenile scombroids later identified as oceanic skipjack, *Katsuwonus pelamis*. One specimen, measuring 130 mm. from the snout to the end of the hypural plate, was found on July 21, 1950, in the stomach of a black marlin (*Makaira mazara*) caught a few days previously in the vicinity of 1°30′ N., 154°08′ E. Two additional juveniles of 132 mm. and 169 mm. were recovered on July 24, 1950, from a sailfish (*Istiophorus orientalis*) captured by longlines near 2°28′ N., 155°01′ E. The remaining four specimens, measuring 81 mm., 94 mm., 132 mm., and 148 mm., were found in stomachs of yellowfin tuna (*Neothunnus macropterus*), the smaller two on August 4, 1950, and the larger two on August 8, 1950. The earlier catches of yellowfin tuna were made at approximately 1°10′ N., 157°29′ E., and the later catches at 1°14′ N., 157°28′ E. Remains of fish up to 250 mm. in size and identified by skeletal characteristics as oceanic skipjack were found in tunas and other pelagic fish but were not retained because of their poor condition.

All of the listed juveniles except the 81-mm. fish were X-rayed in the laboratories of the Pacific Oceanic Fishery Investigations in Honolulu, Hawaii. On negatives taken of these juvenile scombroids the skeletal "trellis" of Kishinouye (1923) (="basketwork" of Godsil and Byers (1944)) was faintly visible in every case and placed these fish within Kishinouye's family Katsuwonidae. The Katsuwonidae include two genera: *Euthynnus*, which is composed of species having either 37 or 39 vertebrae (Kishinouye 1923, Schaefer and Marr 1948b), and *Katsuwonus*, which contains a single species characterized by 41 vertebrae (Kishinouye 1923). There is no knowledge of an overlap in vertebral counts between genera. The total count of 41 vertebrae, including the urostyle, therefore, specifically identified these juveniles as *Katsuwonus pelamis* Linnaeus.

For further verification, the 81-mm. juvenile was stained, using Hollister's method (1934). There are 41 vertebrae present with 20 precaudal and 21 caudal vertebrae. The lateral processes on the precaudal vertebrae are well developed and the inferior foramina form a "trellis" with the haemal arches. The haemal canal is large, and the first closed haemal arch is on the twelfth vertebra. The gill-raker count for the first gill arch on the left side, which is 15 for the upper arch and 38 for the lower, falls within the range of counts given for adults—15 to 20 and 36 to 38, respectively (Kishinouye 1923). Palatine teeth are present; vomerine teeth are absent. Vestigial palatine teeth were observed on the 94-mm. specimen and were absent on the next larger juvenile of 130 mm., so that palatine teeth disappear at a length somewhere between these two.

The presence of juvenile oceanic skipjack in stomachs of fish caught throughout the area fished by vessels of the expedition points to the existence of extensive spawning grounds in or adjacent to these waters. The only previous published record of juvenile skipjack from this general locality is that of Inanami (1942). Since this reference is not generally available, my translation of his paper is given here in full:

When I went to Truk in June of this year, I was shown specimens of small skipjack at the Nankō Fisheries Company. Of the two, one specimen measuring over 6 *sun* (180 mm.) was unmistakably a skipjack juvenile; the other, measuring 1.5 *sun* (45 mm.) in length, may have

been a juvenile skipjack. The following data were gathered for these specimens:

(1) Dimensions: Length, 6.6 *sun* (198 mm.); weight 25 *momme* (94 grams).
Date of capture: 1700, April 23, 1939.
Place of capture: 4 nautical miles southwest of Sarashima Pass (Salat Pass, 7°14′ N., 152°01′ E.).
Method of capture: Pole fishing.
At the same time, a specimen which could have been placed in a rice bowl and assumed to have been about 3 *sun* (90 mm.) in length was caught but not retained owing to the carelessness of a crew member.

(2) Dimensions: Length, 1.5 *sun* (45 mm.): weight, 2 *momme* (8 grams).
Date of capture: May 3, 1940.
Place of capture: 14 nautical miles off Sarashima Pass.
Method of capture: Recovered from the stomach of a skipjack which apparently had been caught immediately after feeding, for there was no evidence of digestion.

It is said that small fish weighing 25 *momme* (94 grams) are extremely rare around Truk, but that fish of this size are often seen around Palau during certain seasons of some years.

Although oceanic skipjack are known to be abundant in the vicinity of the many islands and reefs of the western equatorial region, this species apparently is not landbound, for several schools were seen and fished far from land during the operations of the expedition. Spawning probably takes place in the open ocean, as well as near land, as inferred from the recovery of juveniles in fresh condition from fish caught in deep offshore waters. Judging from the sizes of young skipjack found, some spawning must occur during the spring months. Kishinouye (1924) estimates that young skipjack grow at a rate of more than 40 mm. a month. Calculations based on this growth rate suggest that juveniles recovered aboard the mothership in July were spawned in March and April, and those found later, in April, May, and June.

OCCURRENCE OF BLUEFIN TUNA (*THUNNUS ORIENTALIS*)

The bluefin tunas are generally regarded as temperate-zone forms and are seldom found in tropical waters. The capture of 10 large tunas identified as bluefin or black tuna, probably *Thunnus orientalis* (Temminck and Schlegel), by expedition vessels is therefore of interest (table 3). Furthermore, the frequency with which this species was caught this year indicates a possible change in factors governing its distribution or availability in the western equatorial region. Examination of available published logs covering the prewar activities of Japanese tuna-fishing vessels in the Palau, Mariana, and Caroline Islands failed to show bluefin tuna in their catches. With the exception of Abe's listing (1939) from the Palau Islands of a 240-mm. specimen identified as *Thunnus thynnus* (=*Thunnus orientalis*?), as far as is known, no other distribution records exist for bluefin tuna from this general area.

TABLE 3.—*Bluefin tuna captured in the western equatorial Pacific, June–September 1950*

Fish No.	Date of capture	Locality of capture	
		Latitude	Longitude
1	June 17	4°20′ N.	145°20′ E.
2	June 26	4°30′ N.	145°10′ E.
3	July 5	2°39′ N.	148°40′ E.
4	July 12	4°08′ N.	147°57′ E.
5	July 14	3°48′ N.	147°55′ E.
6	July 19	5°02′ N.	154°16′ E.
7	July 26	2°25′ N.	155°49′ E.
8	Aug. 10	4°00′ N.	157°30′ E.
9	Aug. 12	4°15′ N.	156°19′ E.
10	Sept. 4	2°25′ N.	155°49′ E.

The captured fish were all large and weighed from 150 to 500 pounds eviscerated and with gills removed. Since these fish were cleaned at sea immediately after capture and the viscera discarded, it was not possible to examine the internal organs and gill rakers. The pectoral fins of those individuals examined were comparatively short, and each fish was characterized by a dark over-all coloration, which varied from black dorsally to a dusky gray ventrally. Measurements of different body characters, using standard morphometric techniques described by Marr and Schaefer (1949), were taken of four fish. The data are presented in table 4.

There are three commonly recognized bluefin species inhabiting the Pacific Ocean: the southern bluefin tuna of Australia, *Thunnus maccoyi;* the Japanese bluefin or black tuna, *Thunnus orientalis;* and the so-called California bluefin tuna, *Thunnus thynnus*, which is found in the eastern Pacific and adjacent waters. The presently recognized northernmost limit of distribution of *T. maccoyi* is Sydney, Australia (Serventy 1941). The Japanese bluefin tuna, *T. orientalis*, which has yet to be proved distinct from *T. thynnus*, may occur as far south as the equator, for there are

TABLE 4.—*Measurements of four bluefin tuna from the western equatorial Pacific*

	Fish No. 1	Fish No. 3	Fish No. 5	Fish No. 7
Date of capture	June 17	July 5	July 14	July 26
Locality of capture:				
Latitude	4°20′ N.	2°39′ N.	3°48′ N.	2°25′ N.
Longitude	145°20′ E.	148°40′ E.	147°55′ E.	155°49′ E.
Approximate weight (less viscera and gills) lbs.			487	430
Total length mm.	2,255	2,139	2,239	2,205
Head length mm.	600	582	631	599
Snout to insertion first dorsal mm.	648	624	661	642
Snout to insertion second dorsal mm.	1,221	1,136	1,185	1,172
Snout to insertion anal mm.	1,354	1,253	1,373	1,310
Snout to insertion ventral mm.	696	649	748	674
Ventral insertion to vent [1] mm.	667	632	675	676
Greatest body depth mm.	578	550		
Length pectoral mm.	418	405	405	389
Length second dorsal mm.	441	344	423	377
Length anal mm.	391	331	428	365
Diameter of iris mm.	48	46	51	45

[1] Defined as the distance from a line connecting the insertions of the ventral fins to the anterior edge of the vent.

records of this species from the southern Philippine Islands as cited by Wade (1950b). However, Wade believed that the southern distribution of *T. orientalis* was limited to the northern Philippine Islands and that other records were of stray fish.

The bluefin tuna herein recorded have been assigned to *T. orientalis* on the basis of distribution alone. It may be shown in the future that *T. orientalis* is either a valid species or is synonymous with *T. thynnus*.

SUMMARY

Various biological investigations were conducted aboard a Japanese tuna mothership on tunas and other fishes landed by longline-fishing vessels which operated in waters south of the Caroline Islands during the summer of 1950. The results of these studies shed new light on the spawning and distribution of tuna species found in the western equatorial Pacific.

Gonads of yellowfin tuna and big-eyed tuna were examined for sexual maturity, and their condition suggests the existence of spawning grounds for these two species in or near the region fished. The yellowfin probably spawns most actively during the summer months. Observations of big-eyed tuna lead to the conclusion that this species spawns from June to September, and possibly during other seasons of the year.

Several juvenile oceanic skipjack were recovered from the stomachs of tunas and other pelagic fishes. This is definite proof that oceanic skipjack spawn extensively in or near the area covered by the expedition.

The occurrence of bluefin tuna in equatorial waters is recorded on the basis of several fish caught from June to September 1950.

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UNITED STATES DEPARTMENT OF THE INTERIOR, OSCAR L. CHAPMAN, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

POSTLARVAL *NEOTHUNNUS MACROPTERUS, AUXIS THAZARD,* AND *EUTHYNNUS LINEATUS* FROM THE PACIFIC COAST OF CENTRAL AMERICA

By GILES W. MEAD

Illustrations by Walter B. Schwarz

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CONTENTS

	Page
Observations on adults	121
Observations on young	122
Key to postlarvae of five species of Central American scombrids	122
Neothunnus macropterus (Temminck and Schlegel)	123
Auxis thazard Lacépède	124
Euthynnus lineatus Kishinouye	126
Literature cited	126

POSTLARVAL *NEOTHUNNUS MACROPTERUS, AUXIS THAZARD,* AND *EUTHYNNUS LINEATUS* FROM THE PACIFIC COAST OF CENTRAL AMERICA

By GILES W. MEAD, *Fishery Research Biologist*

Until 1942, none of the spawning areas of the several species of eastern Pacific tunas was known. Since that year several such regions have been identified and in each case the discovery has been made by indirect means, through the collection and identification of the pelagic postlarvae, for the ripe eggs of the tuna have rarely been found. Knowledge of the location and extent of the spawning grounds of the tunas depends, therefore, on being able to identify the young taken in plankton collections. This paper provides a description of the identifying characters of the juveniles of several tunas.

In the late spring of 1949 I had the opportunity to make collections of pelagic postlarvae in waters off the Pacific coast of Central America. Supplementing this material, a series of uncatalogued specimens [1] from the California Academy of Sciences, which was collected off Central America during the 1932 cruise of the *Zaca,* was examined.

OBSERVATIONS ON ADULTS

The fishes collected in the spring of 1949 were taken from the motor vessel *Alphecca,* a tuna clipper fishing for the Westgate–Sun Harbor Co. of San Diego, Calif. Actual fishing was confined to the month of May in waters from 50 to 150 miles off the west coast of Nicaragua and El Salvador. During this period the 240-ton catch consisted of yellowfin tuna, *Neothunnus macropterus* (Temminck and Schlegel), and oceanic skipjack, *Katsuwonus pelamis* (Linnaeus), the former comprising the bulk of the catch by weight and number. Gonads of 25 of each species were examined for degree of maturity. It was apparent from this examination that the yellowfin tuna more than 75 centimeters long and all the oceanic skipjack were in advanced stages of sexual maturity. (Total lengths are taken from tip of snout to distal end of the shortest caudal fin ray.) Ovaries were swollen and turgid, although no ova were visible to the unaided eye. Testes of both yellowfin tuna and oceanic skipjack had milt in the central duct. Several large male yellowfin were running ripe, but no females in a similar condition were observed in the catch. Two female black skipjack, *Euthynnus lineatus* Kishinouye, 54.4 and 55.0 cm. in length were taken. Their ovaries were similar in degree of maturity to those of the oceanic skipjack. Two ripe female sierra mackerel, *Scomberomorus sierra* Jordan and Starks, were taken in a bait haul at Macapule, Mexico, in the Gulf of California. Eckles (1949) has described the postlarvae of this species. Although numerous attempts were made with a high-speed plankton net to recover the eggs from the surface layers of waters where mature fish were found, none proved successful.

Apparently the spawning season for the tunas is a long one and the spawning area large. Ehrenbaum (1924) outlines the probable spawning grounds in the Mediterranean region and in the Atlantic for the species represented in his collections by larvae and postlarvae. He also describes the degree of maturity and possible migrational routes of the adults. Similarly, various Japanese workers have attempted to delimit spawning areas in the western Pacific, and at present extensive work is being done near the Hawaiian Islands and the Philippines. The spawning areas of the tunas in Central America are now known to extend from Panama north to Nicaragua and El Salvador and off shore to a distance of more than 100 miles. It is also probable that spawning of yellowfin tuna and oceanic skipjack occurs off Mexico, since the *Zaca* collections made there include frigate mackerel and one larval black skipjack. It is not unlikely that future work will show that this spawning area extends throughout the tropical waters of Central America.

[1] Made available by Lillian Dempster of the California Academy of Sciences.

OBSERVATIONS ON YOUNG

Since the tunas are subject to intensive fishing in many parts of the world their biology has long been under investigation. Kishinouye (1919) outlines the early work done on the larval stages of these fishes. As he points out in another paper (1926), the work of Ehrenbaum (1924) is probably the most important single work on the young stages of these fishes. The fishes described by Ehrenbaum (1924), Kishinouye (1926), Lütken (1880) and other early workers were generally less than 15 millimeters in length and were taken with plankton nets. For the larger sizes the investigator is dependent primarily on collections made under lights or on specimens found in the stomachs of adult fish. Such specimens as these have been described by the more recent workers, Schaefer and Marr (1948a, 1948b), Eckles (1949), Wade (1949), and others. In this paper I shall describe specimens principally between 10 mm. and 18 mm. in length, larger than those taken in plankton hauls, and note characters I have found useful in their identification.

As is generally the practice, the *Alphecca* often drifted at night while on the fishing grounds, offering an excellent opportunity for night collecting. The collections were made under a droplight suspended immediately above the water. Fourteen such collections yielded, among others, juveniles of the following three scombrid fishes: *Neothunnus macropterus*, the yellowfin tuna; *Euthynnus lineatus*, the black skipjack; and *Auxis thazard*, the frigate mackerel. Early stages of all these species have been described by Schaefer and Marr (1948a, 1948b) from specimens taken in the spring of 1947 off Central America. The identification of their specimens made known spawning grounds for the yellowfin tuna, oceanic skipjack, black skipjack, and frigate mackerel off Costa Rica and Panama. The present collections extend the known limits of these spawning regions for three of these species 350 miles northwest up the Central American coast. Dates, positions, and other data for the collections are reported in table 1.

TABLE 1.—*Data on postlarval* Auxis thazard, Neothunnus macropterus, *and* Euthynnus lineatus *taken from the Pacific Ocean off Central America, May 1949*

Date	Location		Species	Number of specimens	Length in millimeters
	Latitude	Longitude			
May 7	11°23′N.	90°29.5′W.	A. thazard	28	10.5 to 28.5
May 10	10°58′N.	89°56′W.	A. thazard	2	10.0 to 28.0
			E. lineatus	2	7.5 to 10.5
May 15	11°46′N.	87°28′W.	A. thazard	3	11.5 to 35.0
May 16	11°46′N.	87°41′W.	A. thazard	2	27.0 to 30.0
May 17	12°16′N.	89°31′W.	A. thazard	2	28.0 to 30.0
			N. macropterus	25	15.5 to 25.0
May 19	11°20′N.	87°20′W.	A. thazard	36	14.5 to 31.0
			E. lineatus	23	13.5 to 18.0
May 22	11°26′N.	89°22′W.	A. thazard	15	18.0 to 35.0
May 24	10°47′N.	89°30′W.	A. thazard	57	13.5 to 48.0
May 27	12°50′N.	89°40′W.	A. thazard	1	19.0
			E. lineatus	2	18.0 to 23.5
May 28	11°05′N.	89°55′W.	A. thazard	76	10.5 to 48.5
			N. macropterus	12	10.5 to 16.0
May 29	11°05′N.	89°55′W.	A. thazard	12	19.5 to 35.0
May 30	12°11′N.	90°18′W.	A. thazard	27	24.5 to 40.5
			N. macropterus	5	19.5 to 26.5

KEY TO THE POSTLARVAE OF FIVE SPECIES OF CENTRAL AMERICAN SCOMBRIDS

A workable key for the identification of the postlarvae of scombrids known to occur off Central America is dependent on a few discrete external characters. The teeth and body shapes are similar in all species. Pigmentation, gill rakers, preopercular spines, viscera, and, to some extent, fin rays are in the process of development and show variation within each species at a given length. The characters used in the key presented here were taken from specimens of *Euthynnus lineatus* from 7.5 mm. to 32.5 mm., *Neothunnus macropterus* from 10.5 mm. to 26.5 mm., *Scomberomorus sierra* from 21 mm. to 71 mm., and *Auxis thazard* from 10 mm. to 48.5 mm. in length. The characters used separate species within these ranges but may not hold true for larger or smaller specimens. No specimens of *Katsuwonus pelamis* were examined but the description of Schaefer and Marr (1948b) based on two individuals, 21 mm. and 44 mm. in length, has been referred to in preparation of the key. There is no spot on the isthmus of the smaller of these two specimens. The larger fish was cleared and stained for bone study, thus destroying all pigmentation.

1a. More than 17 spines in the first dorsal. Total number of vertebrae more than 46, usually 47 or 48. First dorsal pigmented distally. Pigment spot on point of isthmus ..... *Scomberomorus sierra.*

1b. Less than 17 spines in first dorsal. Less than 46 vertebrae.

2a. First dorsal separated from the second by a distance equal to or greater than half the length of the first dorsal; usually 11 spines in first dorsal. Spot on isthmus. Vertebral count usually 20+19=39 ..... *Auxis thazard.*

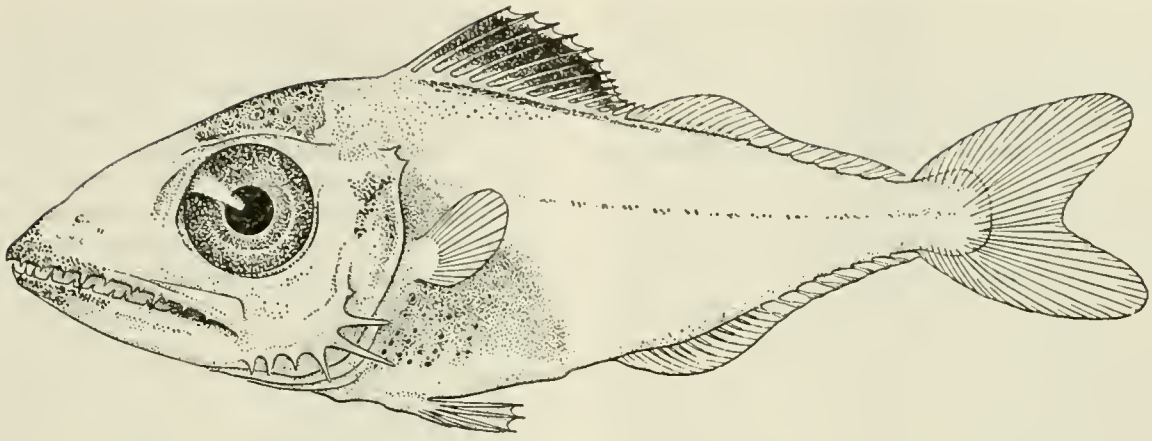

FIGURE 1.—*Neothunnus macropterus*, 10.5 millimeters long.

2b. First dorsal continuous or almost continuous with second dorsal.
3a. Pigment spot on point of isthmus. First dorsal 14 to 16, heavily pigmented. Vertebral count usually 20+17=37. *Euthynnus lineatus.*
3b. No pigment spot on isthmus.
4a. First dorsal 13 or 14, entire fin heavily pigmented. Vertebral count 18+21=39 ---------- *Neothunnus macropterus.*
4b. First dorsal 16, bearing a few moderately large spots distally. Vertebral count 20+21=41 ---------- *Katsuwonus pelamis.*

NEOTHUNNUS MACROPTERUS (Temminck and Schlegel)

A total of 42 specimens of this species was taken in the collection, ranging from 10.5 mm. to 26.5 mm. in length. Representative specimens were cleared with potassium hydroxide and stained with alizarin (Hollister 1934) so that the bone structure could be examined and the fin rays counted. Fin-ray counts in very small specimens are virtually impossible if the specimens are not stained.

Neothunnus macropterus can be identified by its characteristic shape, vertebral count (18+21), and coloration, as described by Schaefer and Marr (1948b). No gill rakers can be seen in fish smaller than 15 mm. The position and extent of the visceral organs cannot be determined without sectioning. Schaefer and Marr (1948b) note the characteristics of the viscera and gill rakers in specimens over 15 mm. With the exception of the pectoral, the fins of a 10.5-mm. fish have within one or two rays of the complete complement of spines or rays. The number of rays in the pectoral fin increases from 13 in the 10.5 mm. specimen to 30 in fish of 30 mm. Each half of the upper and lower jaws bears 11 small, pointed, irregularly spaced teeth. It was found that these young yellowfin can be separated readily from the other species taken, without a special preparation, by the absence of any pigmentation on the point of the isthmus and by the heavily pigmented first dorsal fin. In all *Euthynnus lineatus* and *Auxis thazard* examined there is a pigment spot on the point of the isthmus overlying the junction of the pectoral and pelvic girdles. No postlarval *Katsuwonus pelamis* were available for study, but Milner B. Schaefer of the Pacific Oceanic Fishery Investigations informs me that this spot is not present on a 21-mm. specimen taken off Costa Rica. I have found no reference to this spot in the literature. This character is most useful for separating very small *N. macropterus* and *E. lineatus* since both have a black dorsal fin and they resemble each other closely in body shape until they attain a length greater than 15 mm.

Dermal pigmentation on a 10.5-mm. *Neothunnus macropterus* is restricted to a thin strip along the first dorsal fin insertion, a patch on the tip of the snout and the heavily pigmented first dorsal fin. Subcutaneous pigmentation occurs over the brain and in the peritoneum overlying the dorsal third of the viscera. In an 11-mm. specimen, the thin strip along the first dorsal insertion extends posteriorly to the base of the third ray of the second dorsal fin; by the 12-mm. stage it lines the upper margin of the body from the operculum to the terminal rays of the second dorsal. These two specimens show a faint strip along the postero-ventral margin of the orbit. From this size up to

33 mm., the largest yellowfin examined, the color pattern follows closely the description published by Schaefer and Marr (1948b).

A 12-mm. yellowfin displays three prominent spines at the angle of the preoperculum. Anterior to these are three lesser spines, and three others protrude from the preoperculum above the large spines. With increasing length of fish, all spines become more and more reduced in relation to the size of the head. They are apparently overgrown by the superficial layers of the preopercular bone. In fish of 26 mm., the only spines discernible are those at the angle of the preoperculum, and even these are noticeably less evident. There appears to be little, if any, growth in these spines over the size range of the fish in my collections.

AUXIS THAZARD (Lacépède)

This species is the most numerous in the night collections. Young stages are present in 12 of the 14 collections. The 157 specimens taken range from 10 to 49 mm. in length. In addition to the collections listed in table 1, two larger *Auxis*, 79 and 117 mm. fork length, were taken from the stomach of a large yellowfin caught on May 6 at 11°40′ N. latitude, 91°00′ W. longitude. These two fish, both broken and with the skin and fins digested away, can be recognized as members of the genus *Auxis* by the elongated right lobe of the liver, the total vertebral count (39), and the structure of the individual vertebrae as described by Kishinouye (1923: 460). The gill-raker counts,[2] 10+1+32 and 10+1+33, approximate the counts made by Schaefer and Marr (1948a) on most of their juveniles. In a recent paper, Wade (1949) separates the Philippine species, *Auxis thazard* and *A. tapeinosoma*, on the basis of characters among which only the gill-raker count is applicable to the young stages.[3] He also points out, as Schaefer and Marr (1948a) suggested, that there are probably two species of *Auxis* in Central American waters. If we assume that there are two species and that they can be separated by characters applicable to the Philippine species, my two juveniles, as well as the postlarvae large enough to show a definitive gill-raker count, are *A. thazard*. The gill-raker counts of 10 specimens are given in

[2] The method used in counting and recording gill rakers is the same as that used by Wade (1949) in his discussion of the genus *Auxis*.

[3] Wade's description of *Auxis tapeinosoma* agrees with that of Bleeker (1854). However, the pattern and extent of the corselet scales in Bleeker's figure (1854, pl. 7) of *A. tapeinosoma* agrees more closely with Wade's figure of *A. thazard*.

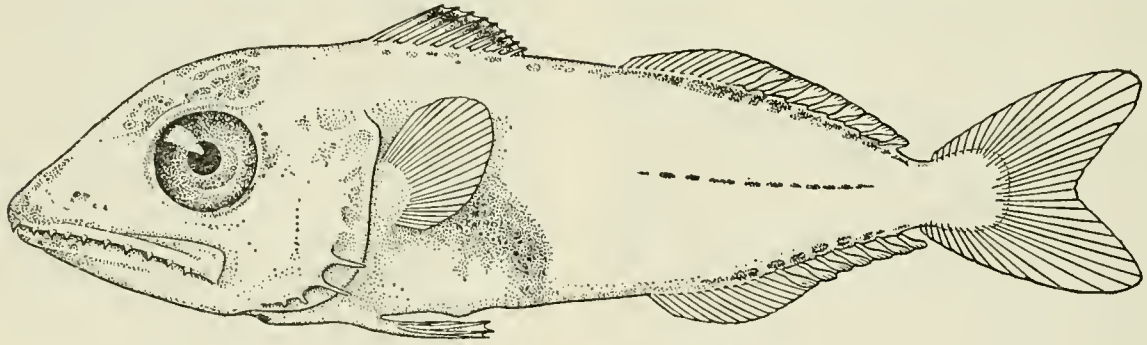

FIGURE 2.—*Auxis thazard*, 11.5 millimeters long.

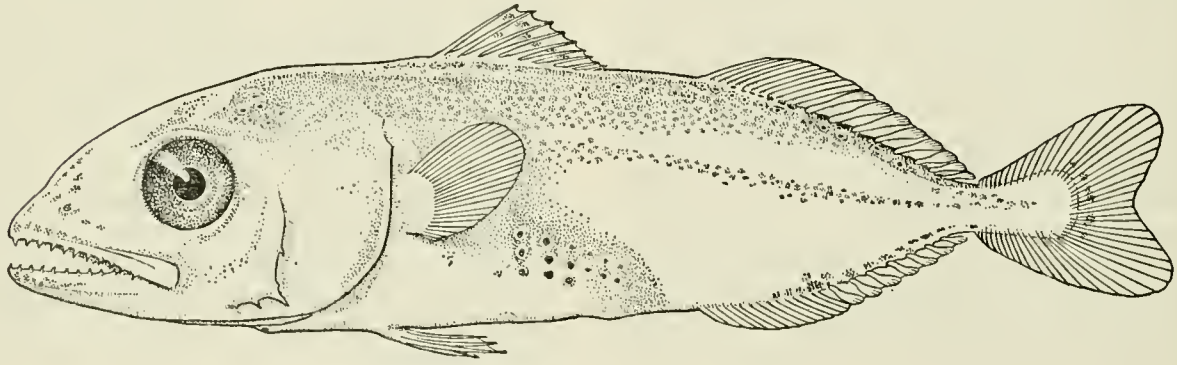

FIGURE 3.—*Auxis thazard*, 18 millimeters long.

table 2. The most anterior arch on both right and left sides was counted. Specimens No. 7 and No. 8 are apparently too small to have a complete set.

TABLE 2.—*Gill-raker counts*[1] *of postlarval and juvenile* Auxis thazard

Specimen	Fork length, in millimeters	Right first arch	Left first arch
No. 1	34	9+1+30=40	8+1+30=39
No. 2	34	8+1+30=39	8+1+29=38
No. 3	41	8+1+31=40	8+1+30=39
No. 4	38	9+1+31=41	7+1+32=40
No. 5	42	9+1+32=42	9+1+31=41
No. 6	35	7+1+30=38	6+1+28=35
No. 7	26	5+1+22=28	4+1+22=27
No. 8	30	7+1+28=36	7+1+26=34
No. 9	79	10+1+32=43	10+1+33=44
No. 10	117	10+1+33=44	10+1+33=44

[1] The method used in counting and recording gill rakers is the same as that used by Wade (1949) in his discussion of the genus *Auxis*.

The smallest *Auxis* in the collections is a damaged 10-mm. specimen. Dermal pigmentation is confined to narrow strips along the bases of the second dorsal and anal fins and the dorsal and anal finlets, along the lateral line from a point below the posterior end of the second dorsal fin to the posterior extent of the finlets, along the posteroventral margin of the orbit and to a small spot on the point of the isthmus. The fins are usually colorless although the first dorsal may bear a few scattered melanophores. Four small spines occur along the angle of the preoperculum. Each half of the upper and lower jaws bears about 10 small teeth. With increasing size of fish, the local centers of pigmentation expand. On fish of 13 mm. the dorsal strip of body pigmentation extends from the operculum to the caudal at its point of least depth, and a light coloration appears on the snout and operculum. All areas in the dorsal half of the body of fish larger than 20 mm. bear at least a light covering of pigment spots. The degree of pigmentation varies greatly from specimen to specimen in this species. The pattern here described is that found to be the most common.

EUTHYNNUS LINEATUS Kishinouye

This species is represented in the collections by 27 specimens, ranging from 7.5 mm. to 23.5 mm. in length. Two fish were cleared and stained and each was found to have a vertebral count of 37, the first caudal vertebra in each case being the twenty-first. As is the case with *Neothunnus macropterus* and *Auxis thazard*, the viscera of the smallest specimens cannot be studied adequately unless specimens are sectioned. Schaefer and Marr (1948a, 1948b) describe the viscera in specimens of *Euthynnus lineatus* more than 15 mm. long. The first dorsal, point of the isthmus, anterior half of the lower jaw, tip of the snout, posteroventral margin of the orbit, and operculum of the smallest specimen (7.5 mm.) bear scattered melanophores. Subcutaneous pigmentation covers the brain and the dorsal margin of the peritoneum. The only dermal pigmentation evident on the body of this specimen is a pair of light spots at the posterior end of the anal fin insertion. At 10.5 mm. in length, light pigmentation appears at the base of the first and second dorsals. Body pigmentation is still confined to the bases of the anal and the two dorsal fins. By 14 mm., the pigment has spread anteriorly from the base of the first dorsal to the area overlying the brain. Coloration along the lateral line first appears in a 16-mm. specimen as a few faint spots. On this fish

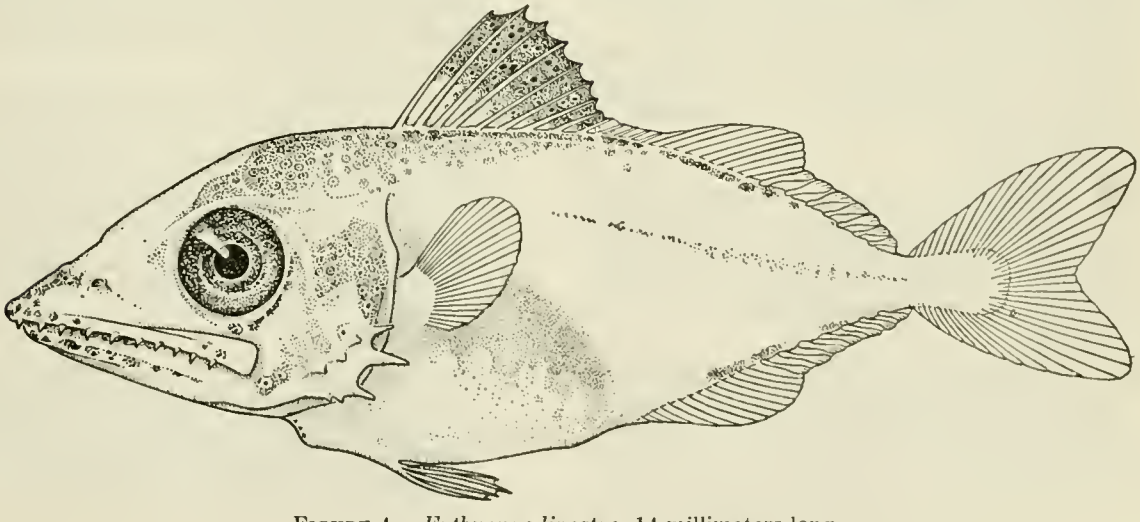

FIGURE 4.—*Euthynnus lineatus*, 14 millimeters long.

the dorsal body pigmentation extends posteriorly from the operculum to the end of the second dorsal. In the region of the second dorsal these spots form a faint line a half millimeter from the dorsal margin of the body. Above this line, along the insertion of the fin itself, is the horizontal bar of dark pigment characteristic of smaller specimens. By 17.5 mm., the lateral pigmentation has extended as far back along the line of the vertebral column as the posterior end of the second dorsal and anal fins. Coloration along the anal insertion is still restricted to the few patches characteristic of the smallest *E. lineatus*. The posterior half of the orbit is dark. Coloration of snout, jaws, and operculum is more dense. At 22 mm., coloration first appears over the terminal segments of the vertebral column and on the extreme base of the median caudal rays. The dorsal half of the body is dark as far back as the caudal peduncle.

Preopercular spines are longer and slenderer than those of *N. macropterus*. The angle of the preoperculum bears the three largest spines. Above these is a pair of small spines; anterior to them are three others. With increasing length of fish, all become overgrown to a certain extent. At 18 mm., the most dorsal and anterior spines are no longer visible without the use of special techniques. The remainder are visible, although less distinct, in the largest *E. lineatus* in the collections.

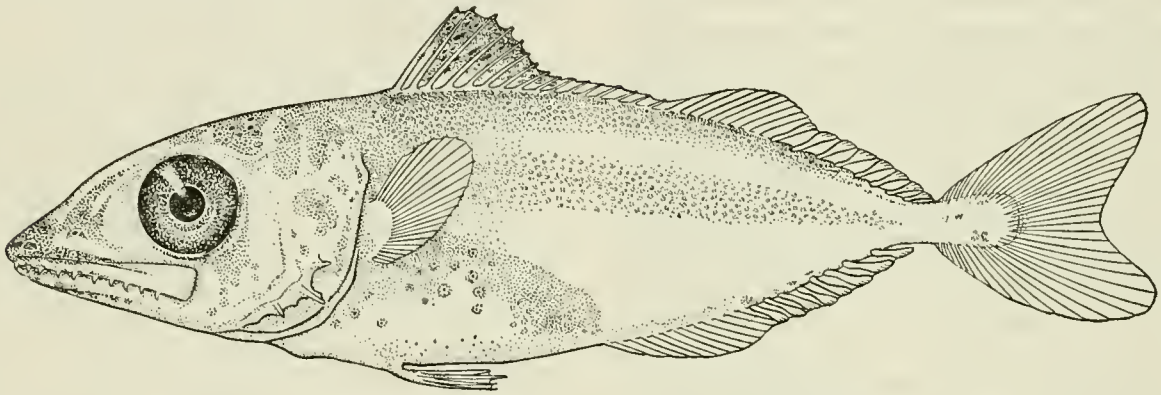

FIGURE 5.—*Euthynnus lineatus*, 22 millimeters long.

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UNITED STATES DEPARTMENT OF THE INTERIOR, OSCAR L. CHAPMAN, *Secretary*
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JUVENILE OCEANIC SKIPJACK FROM THE PHOENIX ISLANDS

By BELL M. SHIMADA

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JUVENILE OCEANIC SKIPJACK FROM THE PHOENIX ISLANDS

By Bell M. Shimada, *Fishery Research Biologist*

Studies by various investigators have added substantially to our hitherto limited knowledge of the spawning of oceanic skipjack (*Katsuwonus pelamis* Linnaeus 1758) in the Pacific Ocean. From evidence based on the examination of gonads or the capture of juveniles (see table), spawning grounds have been indicated in waters off Central America (Schaefer and Marr 1948), the Hawaiian Islands (Eckles 1949), the northern Marshall Islands (Marr 1948), the Truk Islands (Inanami 1942), the Philippine Islands (Wade 1950), and the northern Ryukyu Islands (Kishinouye 1923). The existence of additional spawning grounds near the Phoenix Islands in the south central Pacific is demonstrated by the capture of juveniles incidental to biological, oceanographical, and exploratory-fishing studies conducted in this locality during the summer of 1950 by the Pacific Oceanic Fishery Investigations of the U. S. Fish and Wildlife Service, Honolulu, Hawaii.

During a regular hydrographic cruise of the Pacific Oceanic Fishery Investigations research vessel *Hugh M. Smith*, between Hawaii and the Phoenix Islands, two juvenile scombroids were collected on July 18, 1950, at 3°50.5′ S. and 171°48.5′ W. by collaborating scientist V. E. Brock,[1] and subsequently identified as oceanic skipjack, *Katsuwonus pelamis*. These young fish, measuring 35 mm. and 48 mm. in total length,[2] were captured by dipnet under a night light while the vessel was adrift.

On August 5, 1950, a sister ship, *Henry O'Malley*, visited the Phoenix Islands for exploratory fishing. While night-light collecting from this vessel at a position approximately 400 yards off the west end of Hull Island (4°30′ S., 172°11′ W.), K. Yee,[3] caught three additional specimens of juvenile *K. pelamis*. Total lengths of these fish were 20 mm., 22 mm., and 36 mm.

All five specimens exhibit body contours typical of juvenile oceanic skipjack and possess a very slightly pigmented first dorsal fin and a colorless second dorsal fin, which are characteristic of young fish of this species (Schaefer and Marr 1948, Wade 1950). The 48-mm. juvenile of the *Smith* collection was stained with alizarin red S and found to have a "trellis" and a total of 41 vertebrae, urostyle included. The 20-mm. specimen of the *O'Malley* collection was stained and cleared after Hollister's (1934) method and was found to have a vertebral count of 20+21. These characteristics are definitive of *Katsuwonus pelamis* as shown by Kishinouye (1923), Frade and de Buen (1932), and Godsil and Byers (1944).

The 35-mm. specimen is colored with light-brown pigmentation except for the belly, which is colorless, and the head. Pigmentation is more concentrated dorsally and along the sides of the body where it outlines a narrow band along the midline. Scattered melanophores on the peritoneum are visible through the thin body wall and extend caudally to the anus. The top of the head forward of the nape is brown in color with subcutaneous melanophores on the underlying brain covering. The upper portion of the operculum, the posterior and inferior orbit, as well as the sides of the upper and lower jaw, are lightly pigmented with brown. The membrane between the first and second dorsal spine is irregularly marked with black spots from the base to the distal ends of the spines; the membrane connecting the remaining dorsal spines is similarly marked but only near the tips of the spines, the basal half being colorless. The second dorsal is without color. Black pigment spots are present along the upper pectoral rays and along the upper base of the fin. Similar spots are present along the insertion of the median fins and finlets.

The first dorsal fin is composed of 16 spines of which the second is the longest. Fourteen rays are present in the second dorsal fin. There are 8 dorsal finlets and 7 anal finlets. An interradial

[1] Director, Division of Fish and Game, Territory of Hawaii.

[2] Defined as the distance from the tip of the snout to the tip of the shortest median caudal ray.

[3] Fishery Methods and Equipment Specialist, Pacific Oceanic Fishery Investigations, U. S. Fish and Wildlife Service.

membrane is present in both series of finlets and joins individual finlets at a point midway between the insertion and the tip. The anal fin has 15 soft rays, the pectoral 27 rays, and the pelvic 6 rays. The tip of one large spine and outlines of two additional spines are visible at the angle of the preopercle.

The two smallest specimens, of 20 mm. and 22 mm., agree in general with the description previously given for oceanic skipjack of this size by Schaefer and Marr (1948), but differ in a few respects from the larger juveniles. Body coloration is lighter dorsally, and pigmentation is more intense on the peritoneum. The snout appears to be more sharply pointed, possibly because the upper jaw noticeably overlaps the lower jaw. Two conspicuous spines are present at the bend of the preopercle, and the tip of one additional spine is visible on the inferior margin. Pigmentation of the first dorsal fin is limited to distal ends of the fin membrane between the first and seventh or eighth spine. This is also true of larger specimens, but in the latter coloration extends to the base of the first few anterior spines as well. The basal portion of the pectoral fin is colorless, and the dorsal and anal finlets are joined at the tips by interradial membranes.

The capture of these small juveniles is definite evidence that oceanic skipjack spawn in the Phoenix Islands area.

Published records of juvenile oceanic skipjack (Katsuwonus pelamis *Linnaeus*) *from the Pacific Ocean*

Date of capture	Locality	Size of specimen (mm.)	Number of specimens	How collected	Reference
August 1916	Ryukyu Islands (Okinawa).	210	1	Pole and line (?)	Kishinouye (1923, p. 388).
July 1923	Ryukyu Islands	105	1	From skipjack or yellowfin tuna stomach.	Kishinouye (1924, pp. 88–89).
Do	do	125	1	do	Do.
August 1923	do	210	1	do	Do.
Apr. 14, 1924	Ryukyu Islands (29°47′ N–129°25′ E.)	26	1	From skipjack stomach	Kishinouye (1926, p. 128).
May 16, 1924	Ryukyu Islands (28°10′ N–129°15′ E.)	58	1	From skipjack or yellowfin tuna stomach.	Kishinouye (1924, pp. 88–89).
May 19, 1924	Ryukyu Islands (29°51′ N–129°52′ E.)	60	1	do	Do.
Do	do	80	1	do	Do.
May 21, 1924	Ryukyu Islands (29°47′ N–129°25′ E.)	63	1	do	Do.
Do	do	83	1	do	Do.
Do	do	85	1	do	Do.
May–June 1924	Ryukyu Islands (28°31′ N–129°, 131° E.)	3	2	Plankton net	Kishinouye (1926, p. 128).[1]
Do	do	4	3	do	Do.[1]
June 1924	Ryukyu Islands	120	1	From skipjack or yellowfin tuna stomach.	Kishinouye (1924, pp. 88–89).
Do	do	153	1	do	Do.
Do	do	100 to 140	3	Dipnet	Kishinouye (1926, p. 128).
Apr. 23, 1939	Truk Islands	198	1	Pole-and-line fishing	Inanami (1942, p. 524).
May 3, 1940	do	45	1	From skipjack stomach	Do.[1]
Jan. 28, 1947	Costa Rica (9°22.5′ N.–85°47.5′ W.)	21	1	Dipnet	Schaefer and Marr (1948, p. 193).
Mar. 29, 1947	Costa Rica (9°10′ N–85°20′ W.)	44	1	do	Do.
July 24, 1947	Marshall Islands (Bikini Atoll).	45	1	Regurgitated by skipjack.	Marr (1948, p. 202).
Do	do	50	1	do	Do.
May 7, 1948	Philippine Islands (6°37.2′ N–121°31′ E.)	13 to 27	6	Dipnet	Wade (1950, p. 399).
July 13, 1948	Hawaiian Islands (20°30′ N–158°45′ W.)	113 to 118	6	Regurgitated by skipjack.	Eckles (1949, p. 245).
Sept. 3, 1948	Hawaiian Islands (19°33′ N–156°00′ W.)	183	1	From skipjack stomach	Do.

[1] Identification reported as doubtful.

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UNITED STATES DEPARTMENT OF THE INTERIOR, OSCAR L. CHAPMAN, *Secretary*
FISH AND WILDLIFE SERVICE, ALBERT M. DAY, *Director*

ESTIMATION OF AGE AND GROWTH OF YELLOWFIN TUNA (*NEOTHUNNUS MACROPTERUS*) IN HAWAIIAN WATERS BY SIZE FREQUENCIES

BY HARVEY L. MOORE

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CONTENTS

	Page
Sources of data and methods of collection	134
Analysis of weight frequency data	135
Discussion	141
Conclusions	145
Literature cited	145
Appendix	146

ESTIMATION OF AGE AND GROWTH OF YELLOWFIN TUNA (*NEOTHUNNUS MACROPTERUS*) IN HAWAIIAN WATERS BY SIZE FREQUENCIES

By Harvey L. Moore, *Fishery Research Biologist*

With a commercially important species, such as the yellowfin tuna (*Neothunnes macropterus* Temminck and Schlegel), knowledge of age and growth is essential in both the management and development of a fishery. To be able to assign ages and to determine the rate of growth makes it possible to determine the number and strength of the year classes that comprise the fishable stock. A fishery dependent on a few age groups or year classes is greatly affected by the marked success or failure of the brood produced in any one year. The reduction or increase in numbers is strongly evident in the total catch when that particular year class enters the commercial fishery. If, however, the fishery is composed of many age groups, the success or failure of spawning in any one year will have little effect on the total stock. It is only when there are several consecutive years of marked failure or success that any appreciable differences in numbers are evident.

The vital statistics necessary for quantitative study of fish populations are based on knowledge of the age composition of the stock. It would be difficult indeed to determine such statistics as rates of increase, decrease, fishing, and natural mortality without some knowledge of age and growth. These vital statistics are fundamental in the management of a fish stock.

The age and growth rate of tunas may also be of value in the study of migrations, since it seems logical to expect, in general, that short-lived, fast-growing fish travel shorter distances than fish which are long lived and slow growing.

Since Petersen's first application of the method of size-frequency study to age and growth determination of plaice (1922) many such studies of different species have been made. Much improvement in the original method has been made, and the application of mathematical formulae to describe the growth of fishes has contributed much toward its refinement.

Application of length- or weight-frequency anatysis to study of growth of tunas has been limited. Kimura (1932) calculated growth curves for bluefin (*Thunnus orientalis*) and yellowfin (*Neothunnus macropterus*) from weight frequencies of fish taken in Japanese waters from 1924 to 1931. Although the data were collected over a long period of time, those for yellowfin were based on a few specimens if all data were included in the graphs. An examination of the data, as presented, shows that the values plotted in the graphs are based on a few specimens of yellowfin.

Westman and Gilbert (1941) employed length-frequency distributions in their study of the Atlantic bluefin (*Thunnus thynnus*). The ages of bluefin as determined by this work were based primarily on scale readings although the conclusions were correlated with the results of the length frequencies. Westman and Neville (1942), in another study of the Atlantic bluefin tuna, used length frequencies of tuna samples from chumming and trolling catches made during August and September 1941. The results of this study were also correlated with scale readings. Brock (1944) applied the method of length frequencies in a study of albacore (*Germo alalunga*) taken in the North Pacific and was able to demonstrate the growth of size groups through the albacore season. Partlo (1950) has produced weight-frequency distributions of albacore (*Thunnus alalunga*) taken in the waters of British Columbia during 1949. Sampling was not sufficient to show changes in length throughout the albacore season, but the frequency distributions show the definite size groups which make up the fishery. Okamoto (1940) applied Petersen's method to weight data of skipjack (*Katsuwonus vagans*) taken in Japanese waters. It was possible to follow definite modal groups through 5 months of the fishing season. The question whether modes represented age groups or whether they represented different

strains of skipjack was raised. The conclusion was in favor of age groups.

There has been little study of age and growth determination of Hawaiian tunas. Some measurements of the skipjack (*Katsuwonus pelamis*) were collected by Bonham (1946) in 1944 and 1945, and length frequencies were plotted from these data. Bonham suggested the possibility that two successive year classes were present, but recognized the limitations of his data and did not attempt to assign ages. Brock (ms.) made a rather detailed study of size frequencies of skipjack. He was able to identify modal groups in the catches of successive years and to demonstrate progression of the modes during the year, whence he concludes they are year classes. No previous studies have been made of the Hawaiian yellowfin tuna.

SOURCES OF DATA AND METHODS OF COLLECTION

The data for this study were obtained from two different types of fishery, the long-line or flag-line fishery, and the pole or live-bait fishery. The long-line fishery in Hawaii is carried on throughout the year in most of the waters around the main Hawaiian Islands. The catch from this fishery is sold primarily to the fresh-fish markets by auction. The live-bait fishery, on the other hand, is more seasonal and the catch is primarily for the cannery, although some of the fish are sold on the fresh-fish market, especially when the cannery is not operating during the slack season.

The long-line fishery is conducted by means of setlines made up of units of gear known as baskets. The term "basket" is derived from woven bamboo baskets in which the units of gear are stowed. A vessel fishes a long-line composed of about 30 baskets, each of which is from 140 to 203 fathoms in length and has 4 to 6 branch lines with hooks. When the baskets are fastened together and the long-line is set, the hooks fish from 30 to 50 fathoms in depth (June 1950).

Long-lines are set in the early morning and are fished only during the daylight hours. Usually a few tunas are taken each day, and the catches may also contain several marlin, swordfish, and sharks. Fish taken by this method are generally large in comparison with those taken in the live-bait fishery. Yellowfin tuna caught by this method average about 140 pounds in weight, and the big-eyed tuna (*Parathunnus sibi*) are heavier. The total landings, by months, vary considerably in both the numbers and the species of fish caught. The yellowfin is the most abundant species taken during the summer months, and the big-eyed tuna dominates the winter catch. Albacore also are caught on the long-lines during the winter months, but the numbers are small in comparison with either of the other two species. Although the tunas are definitely seasonal in availability, some fish of all three species usually are taken during the entire year.

The second source of data was the live-bait fishery. This fishery is seasonal; most of the catch is taken during the summer months. The fishery is dependent on small live fishes which are used as chum to lure the tunas within reach of the feather lures or live bait on hooks on the poles of the fishermen. The fish caught by this method are much smaller than those taken by the long-line method; the largest weigh near 25 pounds. The fact that no large fish are caught on the surface by the pole or live-bait fishery and no small fish are caught at depths fished by the long-line gear indicates that there may be a possible vertical migration downward of yellowfin tuna during the early years of life.

Although this fishery is primarily for the skipjack, mixed schools of skipjack and yellowfin or skipjack and big-eyed tuna are sometimes found. Approximately 12 to 15 catches from mixed schools are landed at the cannery each season. It was from schools such as these that the data on small yellowfin were collected for this study. Schools of tuna, whether a pure school of skipjack or mixed with either yellowfin or big-eyed tuna, tend to contain fishes with little range in size. Brock (ms.) says of skipjack schools, "no individual school of fish sampled contained fish differing by more than 20 centimeters in length and usually much less." Differences in sizes of fish from different schools, however, were as much as 50 centimeters.

Weight and length frequencies of the long-line catch were taken from fish sold at auction by the Kyodo Fishing Co., Ltd., Honolulu. The officials of this company were kind enough to allow measuring of the fish on the auction floor before the

bidding had begun. As the fish are sold individually, it is necessary for the company to keep accurate records of the weight of each fish sold. Weights as determined by the auction company were taken from the auction records which were available beginning with November 1947. Weights of tunas caught by the live-bait fishery during 1949 were recorded by Fish and Wildlife Service scientists at the cannery of Hawaiian Tuna Packers, Ltd. This study includes only the data of 1948 and 1949.

The data for the 2 years consist of 4,793 individual weights of yellowfin tuna ranging from 5 to 265 pounds. Of the total number of weights taken, 124 are of small fish most of which were representative of four mixed schools caught by live-bait methods. A few of this group were taken incidentally by trolling or hand-lining. The remainder of the data were obtained from the auction records.

Since small yellowfin and big-eyed tuna are likely to be confused, a check of the reliability of species determination by the auction company was made during October 1949. During this period 95 yellowfin and 272 big-eyed tuna were identified by various Fish and Wildlife Service scientists. In no case was there found to be an auction record in disagreement with our identifications. It was concluded that the assignment of species as shown by the auction records was accurate.

The auction records provided an excellent source of weight-frequency data for several reasons. Because Honolulu is the center of population in the Hawaiian Islands, most of the long-line catch is landed there, and most of this long-line catch passes through the auction of the Kyodo Fishing Co., which supplied the auction records. Fish taken by long-line gear are generally few in number per day's fishing, which would suggest that either the fish tend to be solitary in habit or, if they are schooled, only a few fish from several to many schools are caught during a fishing trip. Since tunas tend to school by size (Brock, in unpublished ms.; Schaefer 1948), samples of this sort which are composed of a few fish from each of many schools will tend to be more nearly representative than large samples drawn from only a few schools as are the samples from the cannery.

Weights of fish in the round, that is, the entire uncleaned fish as landed at the dock, were weighed on the auction company's scales or on those of the Hawaiian Tuna Packers. Weights were recorded to the nearest pound for long-line fish and to the nearest quarter pound for small fish taken by live-bait fishing.

ANALYSIS OF WEIGHT FREQUENCY DATA

The initial step in processing the raw data (see the appendix) was to plot the weights of individual fish as frequency distributions for monthly periods. A class interval of 10 pounds was arbitrarily chosen, with midpoint values of 4.5, 14.5, and so on. Because the monthly catches varied considerably in numbers of fish, they were made comparable by converting the class frequencies into percentages of the total for the month. The average frequency distribution for each year was calculated by averaging the 12 monthly-percentage curves. The results are plotted in figures 1 and 2 for 1948 and 1949. In order to show more clearly the presence of modes, positive deviations from the mean curve for the year are shaded on the graph for each month. The scale at the bottom of each graph is in terms of both weight in pounds and length in centimeters. The length scale was derived from the equation $\log L = 1.45660 + 0.33290 \log W$ which was calculated from a sample of 200 length-weight measurements of yellowfin tuna collected during 1949 by Fish and Wildlife Service scientists.

Because there were many irregularities evident in the frequency curves of each month's catch in both 1948 and 1949, and because the 2 years were similar in monthly frequency distributions, it was convenient to combine the 1948 and 1949 data. The combination of the data for the 2 years was then treated in the same manner as that of the the individual years with the exception of a process of first smoothing the data by the formula $\frac{a+2b+c}{4}$, where a, b, and c, are actual values for consecutive class intervals. After smoothing, the data were transformed into percentages of monthly catch. The resulting monthly distribution curves of the combined data with the superimposed mean-percentage curve for the 2 years calculated in the same manner as for individual years is shown in figure 3.

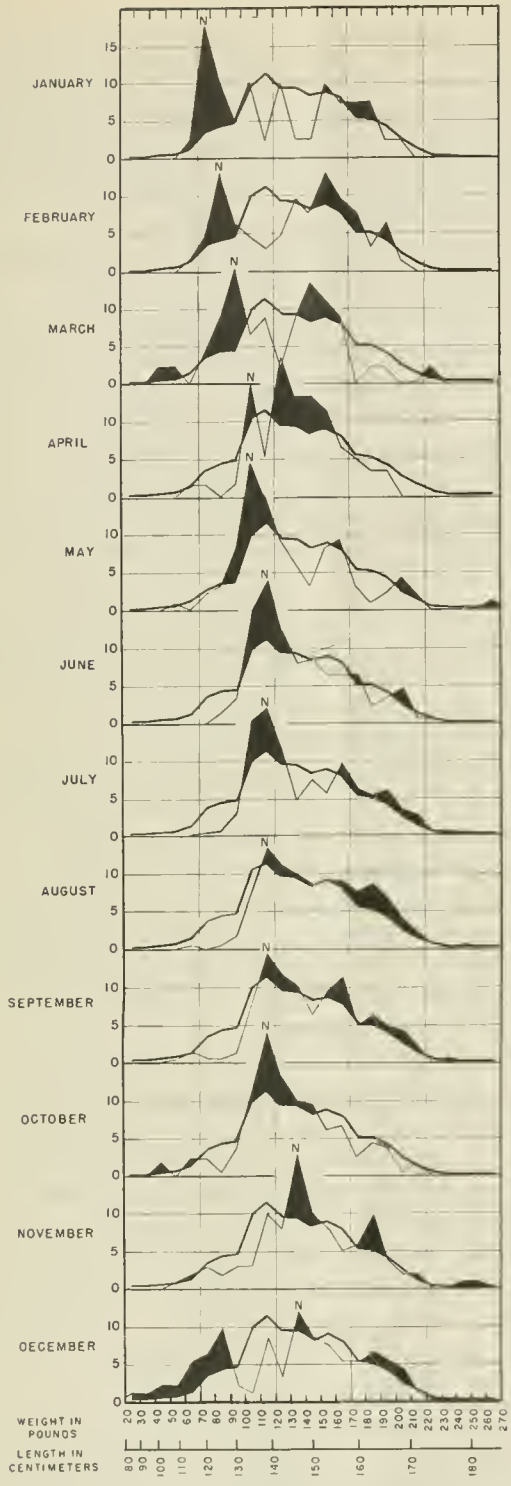

FIGURE 1.—Weight-frequency distributions (in percentage) of long-line catches of yellowfin tuna landed at Honolulu, 1948. Monthly frequency distributions are shown by fine line, and mean monthly frequency distributions by heavy line. Positive deviations from the mean are shaded.

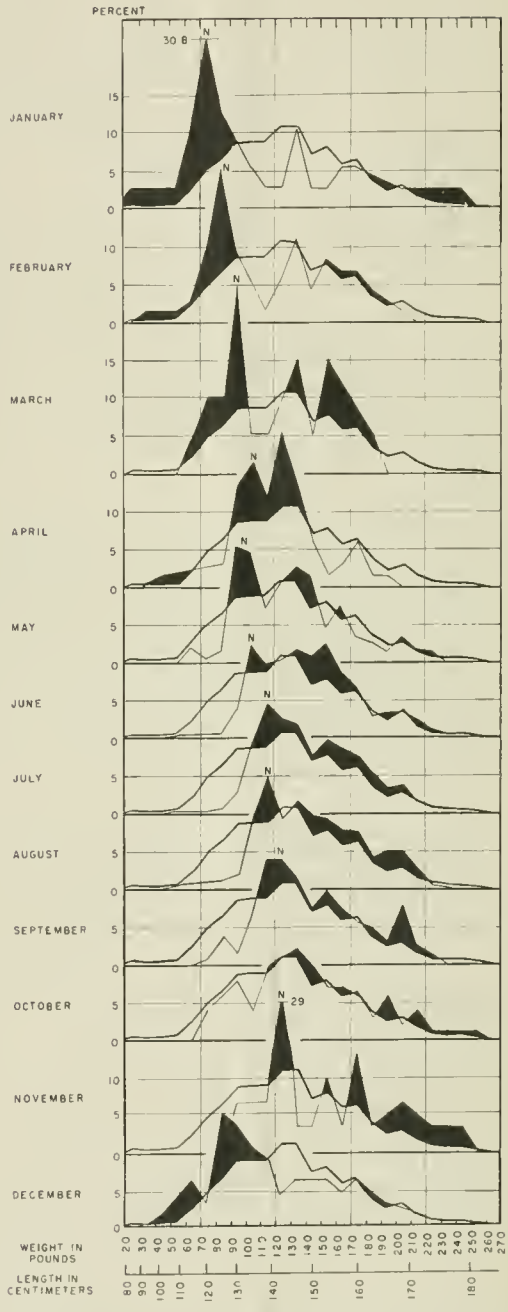

FIGURE 2.—Weight-frequency distributions (in percentage) of long-line catches of yellowfin tuna landed at Honolulu, 1949. Monthly frequency distributions are shown by fine line, and mean monthly frequency distributions by heavy line. Positive deviations from the mean are shaded.

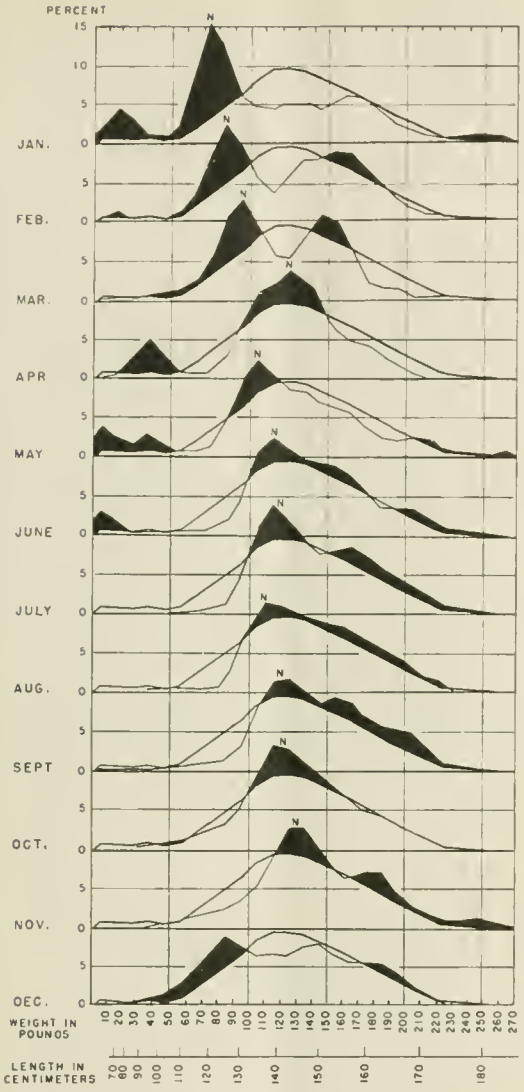

FIGURE 3.—Weight-frequency distributions (in percentage) of long-line and live-bait catches of yellowfin tuna landed at Honolulu. Smoothed data of 1948 and 1949. Monthly frequency distributions are shown by fine line, and mean monthly frequency distributions by heavy line. Positive deviations from the mean are shaded.

Initial examination of the plotted data in figures 1 and 2 shows the presence of a modal group of fishes which can be followed through most months of both 1948 and 1949. The group was designated *N* for reference. In the 1948 data the progression of the modes representing this group indicates gradual growth until June, followed by a 5-month period in which no growth is indicated. Following this there appears to be a short period of rapid growth from October through December. From January through December, modal group *N* shows a gain in weight from 75 to 135 pounds, a gain of 60 pounds in 1 year. Also present in the plotted data is a smaller size group which becomes evident in the long-line fishery in October 1948 and in December 1949. This suggests the entrance of a modal group 1 year younger than group *N*.

The 1949 data (fig. 2) presented a similar trend in modal progression, except for the last 3 months of the year where rather erratic modal peaks were evident. Because the catches for these months were not large in comparison to catches of the summer months (table 1) any unusual distributions of weights of fish landed would cause erratic modal peaks to appear in the percentage frequency distributions.

TABLE 1.—*Numbers of yellowfin tuna taken by long-line fishing and auctioned at the Kyodo Fishing Company, Ltd., Honolulu, in 1948 and 1949*

Month	1948	1949
January	40	39
February	61	73
March	45	20
April	60	67
May	97	158
June	362	514
July	530	545
August	542	400
September	381	165
October	179	102
November	99	31
December	92	67
Total	2,488	2,181

For a more detailed study of the combined data of the 2 years, a criterion was set up to determine what should be designated a mode and to designate its position. . Modal peaks of positive deviations, evident in the combined 2-year data, when plotted as deviations from the mean curve (fig. 4) which met either of the two following conditions were treated as modes in this study:

(1) Any positive deviation of a class which shows a difference of 0.5 or more from values of both adjacent classes (fig. 5–A).

(2) When the difference between frequency values of positive deviations of two adjacent classes is less than 0.5, and when the frequency values of the classes above and below these two adjacent values are at least 0.5 less than the adjacent values, the intersection of the extrapolation of the lines connecting the two classes with the adjacent classes was considered the position of the mode (fig. 5–B).

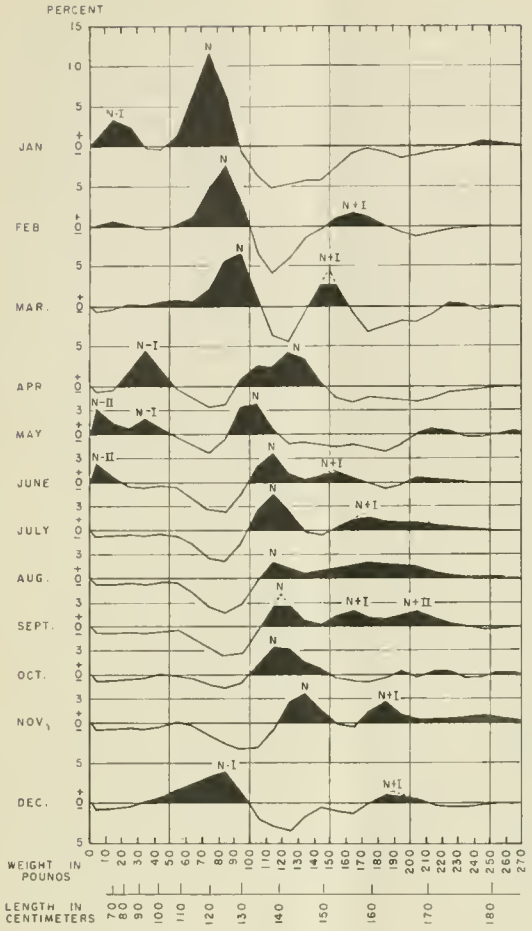

FIGURE 4.—Deviations of monthly frequency distribution from the mean monthly frequency distribution (in percentage) for combined and smoothed 1948 and 1949 data.

Using the above criterion, values of modes were selected as shown in figure 6. Each mode has been labeled with the age group to which it was presumed to belong. In order to plot modal positions against successive months, January of group N was arbitrarily assumed to occur in month 37. Thus the mode of group N in February, March, April, and so on, was plotted in figure 5 against 38, 39, 40, and so on. Modes corresponding to groups which are presumed to be a year younger or older were then plotted 12 months above or below the month value corresponding to group N.

Assuming group $N-I$ to be 1 year younger than N and group $N+I$ to be 1 year older, $N+II$ 2 years older, and so on, we proceeded to determine whether a regular growth curve fitted the data. This was done by the "transformation" method of Walford (1946). This is a graphic method of describing the growth of animals above the point of inflection, the self-inhibiting phase of growth.

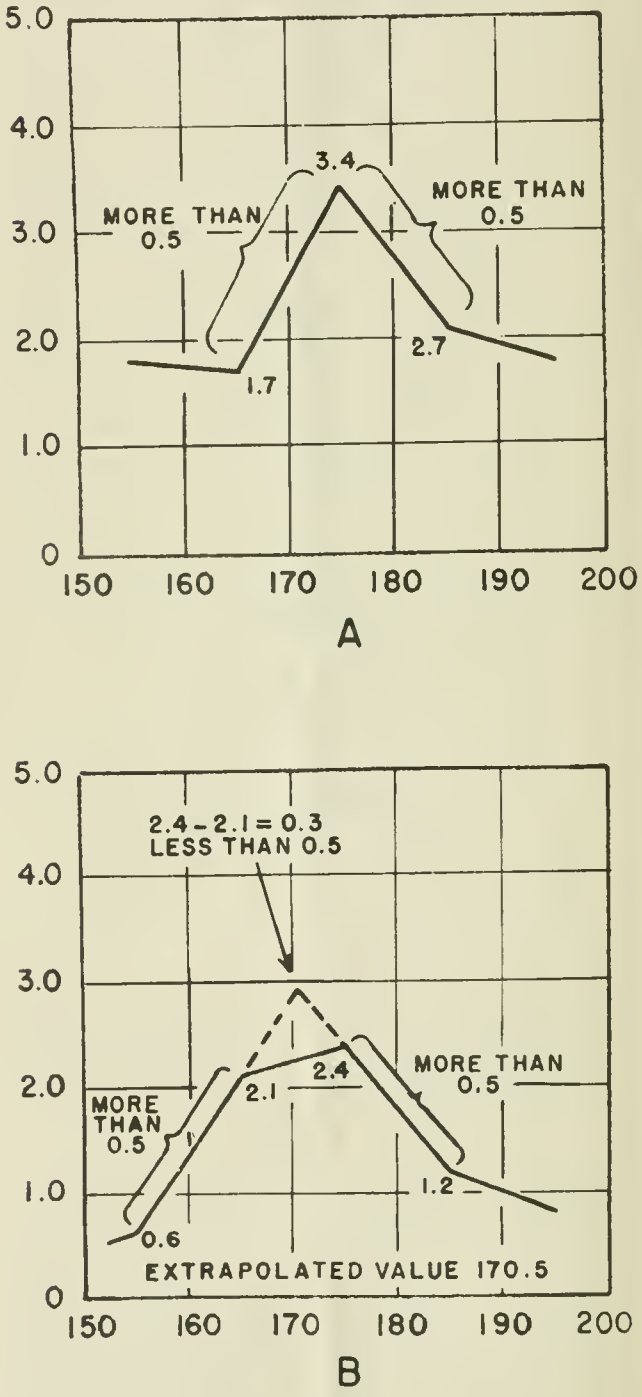

FIGURE 5.—Theoretical conditions demonstrating the criterion used in selection of modes.

Size of fish in figure 6 was plotted in terms of length rather than weight since this method of fitting a growth curve is applicable to sizes above the inflection point. It was obvious from a plot in terms of weights (fig. 9) that the inflection point is within the range of our data, whereas our data in terms of length appear to be above the inflection point.

For the growth of a number of species of animals, Walford's graphic transformation method gives a straight line when the lengths at age 1, 2, 3, 4, . . . n, represented on the x axis, are plotted against the lengths at age 2, 3, 4, 5, . . . $n+1$, on the y axis. This method assumes the growth during each period to be of constant ratio to that of the previous period. It has already been noted that the modes make all their progress during half the year and none in the remainder. This should and does show as a stepwise or sinuous deviation from the straight line. Also, this method requires length values for each consecutive unit of time, in this case for each month. Within the limits of our data (fig. 6) there were 28 months for which no modal values were evident in the plotted data. To furnish estimates of the missing values, linear interpolations were made between observed monthly values.

The series of actual values and interpolated values was then smoothed twice by a running average of three and resulting values of length at age n were plotted against lengths at age $n+1$ where age is in months. The plotted data are well fitted by the least-squares line $Y=7.04-0.96336\ X$, where Y is length at age $n+1$, and X is length at age n (fig. 7). From this straight line the upper limit of growth or the upper asymptote can be derived according to Walford's method by taking the point of intersection of the line fitted to the plotted data and the line of no growth represented by a line of slope 45° through the zero point (fig. 7). In the case of the yellowfin tuna data used herein, the value in length at the point of intersection of the two lines is at 190.0 centimeters, which in terms of weight is equal to 294.9 pounds. A maximum weight of this magnitude is within reason for this species; several specimens approaching this limit have been taken in the local flag-line fishery. The largest specimens included in this study, however, were between 260 and 269 pounds.

Because the plot of n against $n+1$ is a constant-percentage rate and not actual-length values, it is possible to choose the point through which the curve should be passed. As the period from

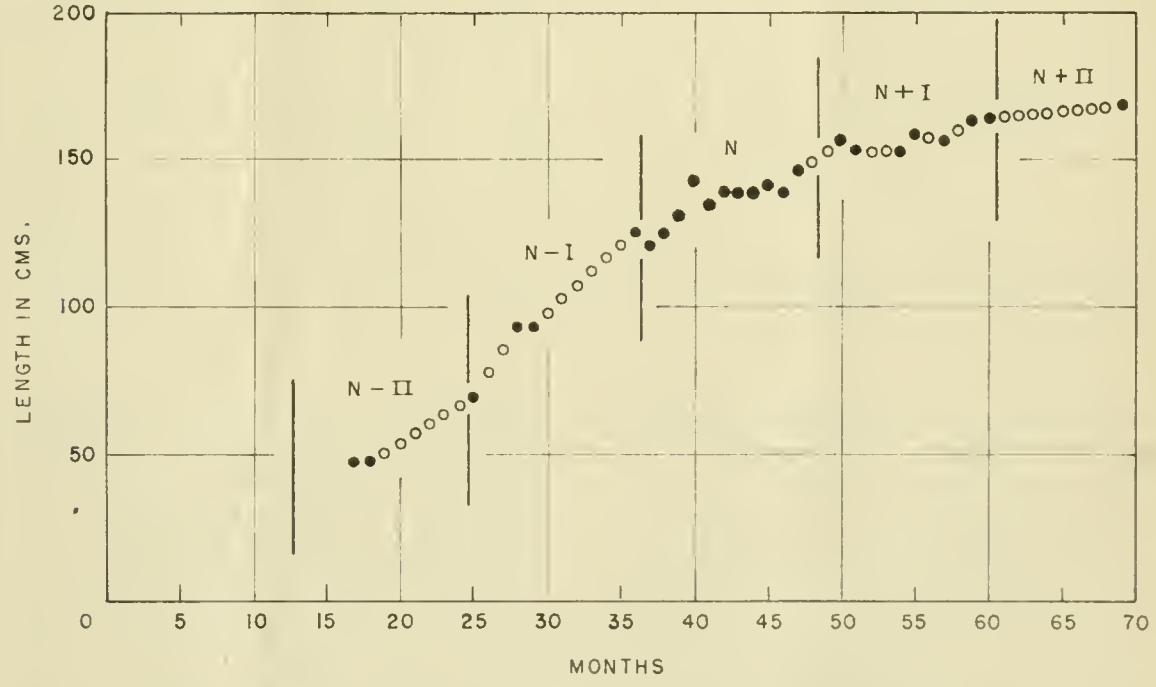

FIGURE 6.— Actual and interpolated values in length plotted against months and showing assigned modal groups. Solid points are actual values and circles are interpolated values. From combined and smoothed 1948 and 1949 data.

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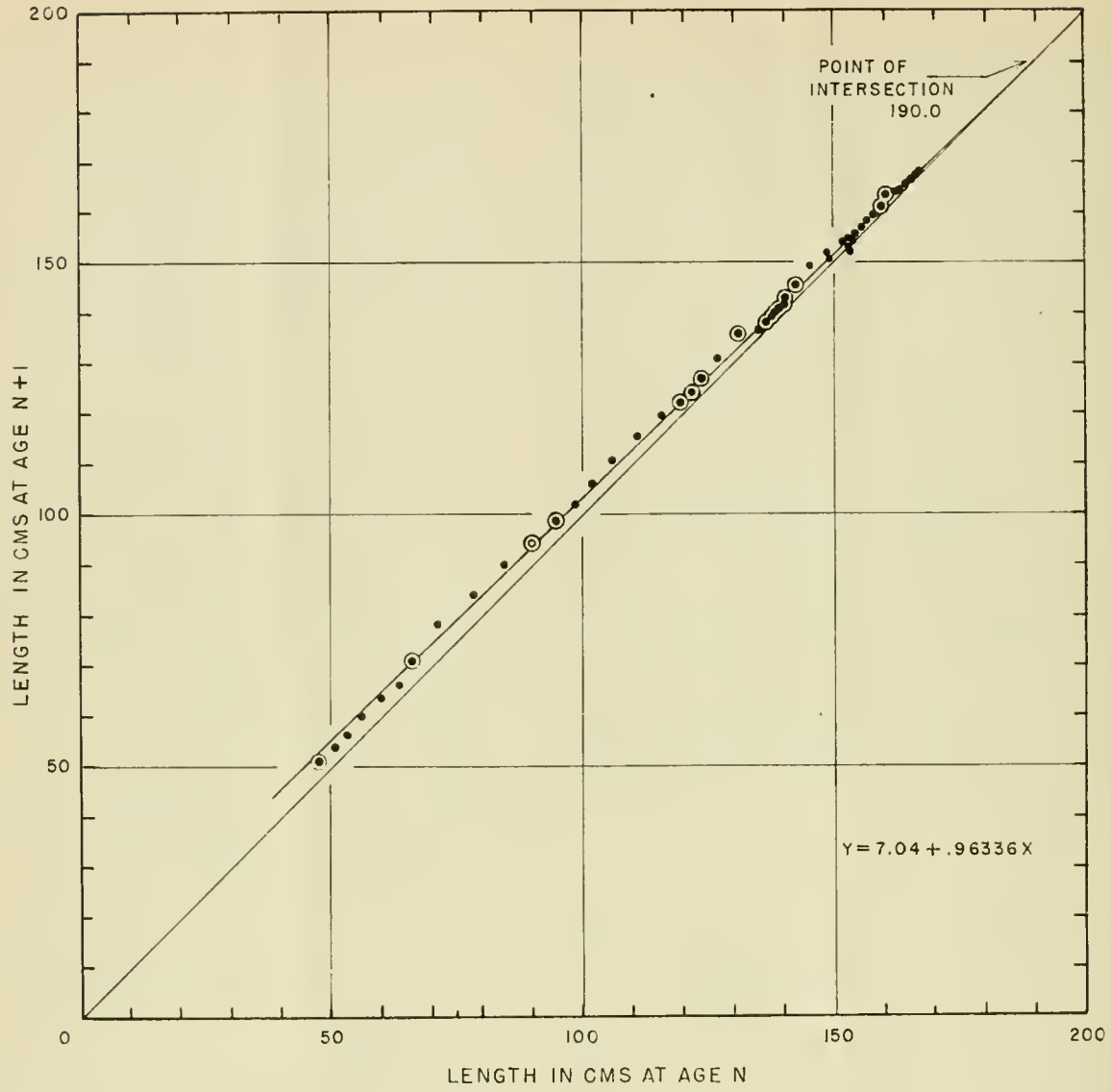

FIGURE 7.—Combined 1948 and 1949 length data are plotted by the method of Walford (1946) and fitted with a straight line. The intersect of the straight line and the line at 45° through the zero point indicates the upper asymptote of the yellowfin tuna. Points marked by ⊙ are observed values.

month 37 through month 47 is the time group N and is most evident in the plotted data, the mean month and mean length of fish occurring in this period were used as the initial point for computing the relation between fish length and time.

The reconstructed growth curve of length on time and the plotted values of the original modes are shown in figure 8. Since figures 7 and 8 indicate that the position of plotted mode values are well fitted by the calculated growth curve, this serves as verification of the assumption that modal group $N-I$ is a year younger than N, group $N+I$ is a year older than N, and so on, is correct. Since the original data were in terms of weight, the calculated curve was also transformed back to those terms. The growth curve of weight on time is shown in figure 9.

From the results of figures 8 and 9, it is possible to determine approximate age of fishes. Extrapolation of the curves downward suggests the origin of the fish to be in year $N-III$. Examination of the gonads of yellowfin taken in local waters indicates the spawning period to be centered about the summer months. Assuming

this to be true, the month of June may be selected to represent the mean spawning period; thus, the period from June N—III to June N—II represents age group O, or fish in their first year of life, June N—II to June N—I, age group I, and so on. Owing to possible error in extrapolating the curves downward to the origin, the ages thus assigned may not be quite correct. It is felt, however, that ages through group IV cannot be more than 1 year in error.

Sella (1929) states that bluefin tuna hatched in June weigh 300 to 500 grams by September. This is a weight of approximately 1 pound and would fall very close to our growth curve as calculated. Kishinouye (1923) says of the common tunny (*Thunnus orientalis*), "such small individuals are found in August and in September. Some of them grow to a length of 30 cm. or more. By next spring they grow to a length of ca 60 cm. When 2 years old they are about 1 meter in length and 11 kg. in weight." These values when plotted on our curve are not much in disagreement. Specimens of yellowfin tuna have been taken during the month of December in Hawaiian waters weighing 2 pounds; these weights when plotted, also fall very close to the curve of figure 9. Lengths and weights by age groups may also be assigned from figures 8 and 9 as has been done in table 2.

TABLE 2.—*Lengths and weights by age groups of yellowfin tuna taken in Hawaiian waters determined by the method of growth analysis of Walford (1946)*

Age group	Length in centimeters	Weight in pounds
0	Less than 54	Less than 7.
I	54–103	7–46.
II	103–136	46–108.
III	136–155	108–163.
IV	155–168	163–208.

DISCUSSION

In fairly close agreement with this study are the observations of Schaefer (1948) of the yellowfin in the waters off Central America, where modes in length-frequency distributions were observed at approximately 60 cm., 85 cm., and 115 cm. These modes, when plotted against the assumed age and the month at which the fish were taken, showed a close similarity to the age-length curve of the Hawaiian yellowfin (fig. 10). The conclusion of

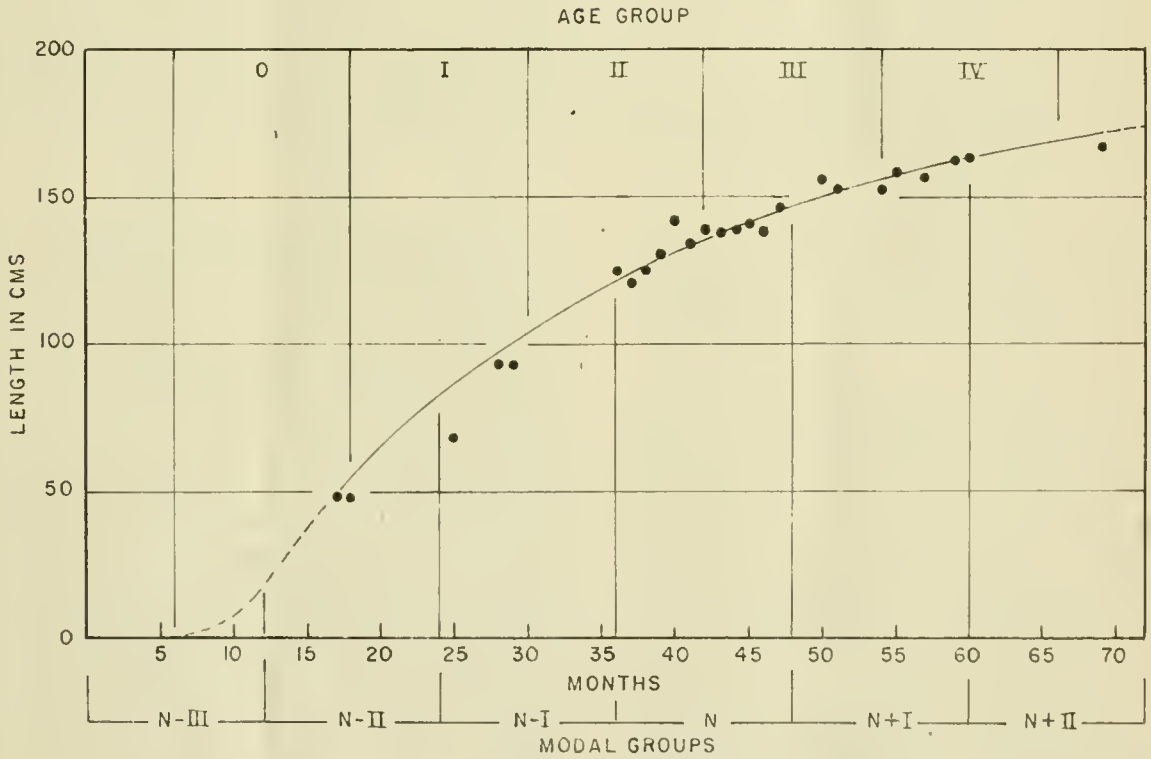

FIGURE 8.—Growth curve of yellowfin tuna taken in Hawaiian waters fitted to lengths with actual modal values in length superimposed.

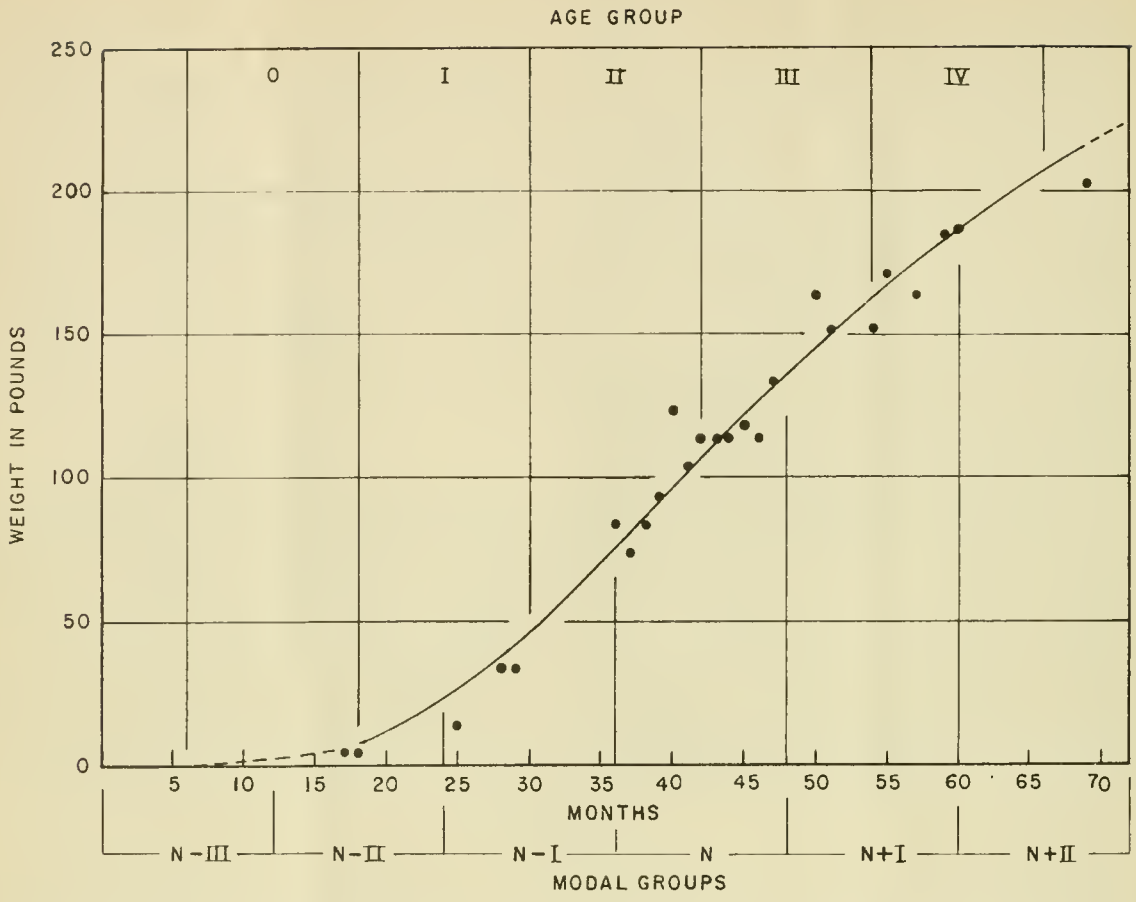

FIGURE 9.—Growth curve of yellowfin tuna taken in Hawaiian waters fitted to lengths and transformed into terms of weight. Actual modal values in weight are superimposed.

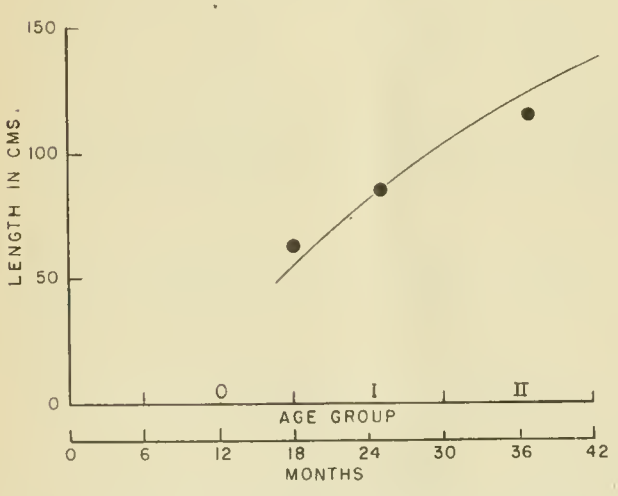

FIGURE 10.—Lengths of dominant size groups of yellowfin taken in waters off Central America by Schaefer (1948) plotted against calculated growth curve of Hawaiian yellowfin.

Schaefer that the 60-cm. fish probably are 1 year old and the 85-cm. fish a year older is also in close agreement.

Our growth curve indicates that the yellowfin tuna grows rapidly during at least the earlier years of life. Group *N* demonstrates a gain in weight of approximately 60 pounds in 1 year. Aikawa and Kato (1938) and Kimura (1932) have studied age and growth of the yellowfin tuna in Japanese waters. Aikawa and Kato assigned ages by the study of marks on vertebral centra which they considered to be annuli. The resulting age-weight relation is shown in figure 11. In plotting these data, which are from table 3, it was assumed that the maximum values were representative of the end of the year of life because the length and weight values for age group O were maximum values. As the month of June has been used in our study as being the approximate center of the

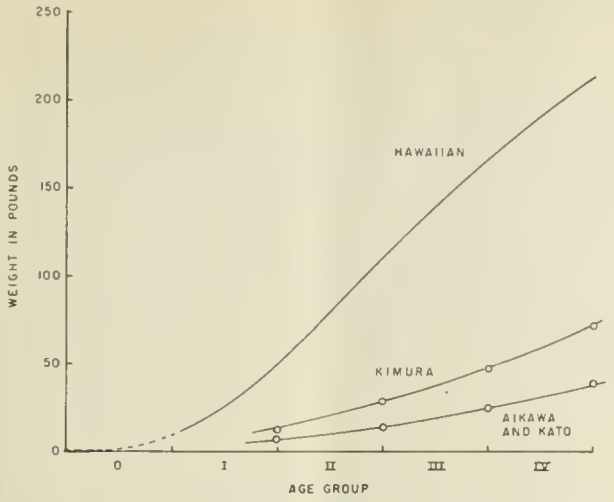

FIGURE 11.—Growth in weight plotted against age for Hawaiian yellowfin as compared to growth curves calculated by Aikawa and Kato (1938) and Kimura (1932).

spawning period, the maximum values as given by Aikawa and Kato have been plotted for the month of June, the assumed last month for any age group. Regardless of the month of the year these values are plotted against, the values for any given age group differ greatly from the values resulting from our study of the Hawaiian yellowfin.

TABLE 3.—*Age, length, and weight range of yellowfin tuna from Japanese waters, from Aikawa and Kato (1938)*

Age group	Length in centimeters	Weight in kilograms	Weight in pounds
0	Less than 38	Less than 1.5	Less than 3.3.
I	38 to 54	1.5 to 4.3	3.3 to 9.5.
II	54 to 70	4.3 to 8.6	9.5 to 19.0.
III	70 to 85	8.6 to 14.0	19.0 to 30.9.
IV	85 to 100	14.0 to 21.4	30.9 to 47.2.
V	100 to 115	21.4 to 34.0	47.2 to 75.0.
VI	115 to 130	34.0 to 44.0	75.0 to 97.0.
VII	130 to 145	44.0 to 57.5	97.0 to 126.8.
VIII	145 to 160	57.5 to 75.0	126.8 to 165.4.

The results of Kimura's (1932) age-weight study also are shown in figure 11. This study is based on a few specimens taken over a long period with no defined method of determining modal values in frequency distributions. The presentation of Kimura's data is based on values of weight taken directly from his growth curve shown in figure 12. Values were converted to pounds for comparison with our data. This growth curve demonstrates more rapid growth than the curve of Aikawa and Kato but still does not agree with the present Hawaiian study.

Figure 13 gives growth curves of other species of tuna taken from various areas in the world compared to the growth curve of Hawaiian yellowfin. We have plotted these from the published data. This graph shows no other tunas as having a growth rate as rapid as that of the yellowfin tuna of Hawaiian waters. The curve of bluefin tuna of the Mediterranean Sea (Sella 1929) is based on more than 1,500 vertebrae samples. This growth curve, like the growth curve of yellowfin based on vertebra-centra analysis (Aikawa and Kato 1938), shows a very slow growth rate and infers a very long-lived fish, for most of the plotted data are below the point of inflection.

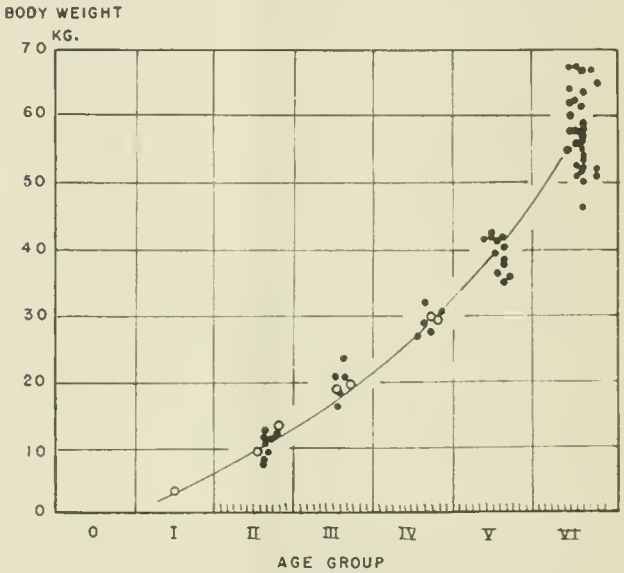

FIGURE 12.—Growth curve of yellowfin tuna in Japanese waters from Kimura (1932). Circles show average weight of a large number of fish of roughly equal weight taken at one time. Solid dots are weights of single fish.

Aikawa and Kato (1938), in addition to their study of the yellowfin, determined ages and growth of the black tuna (*Thunnus orientalis*), the bonito or skipjack (*Katsuwonus vagans*), and the albacore (*Germo germo*) by vertebral-centra analysis. Because the skipjack and albacore are smaller species of tuna not comparable to the yellowfin, they have not been included in the graph. The growth curve of the black tuna, a species more comparable in size, indicates a more rapid growth rate but the curve has only the slightest suggestion of an inflection point. The growth curve of bluefin tuna (black tuna of Aikawa and Kato, *Thunnus orientalis*) by Kimura (1932) from weight frequencies

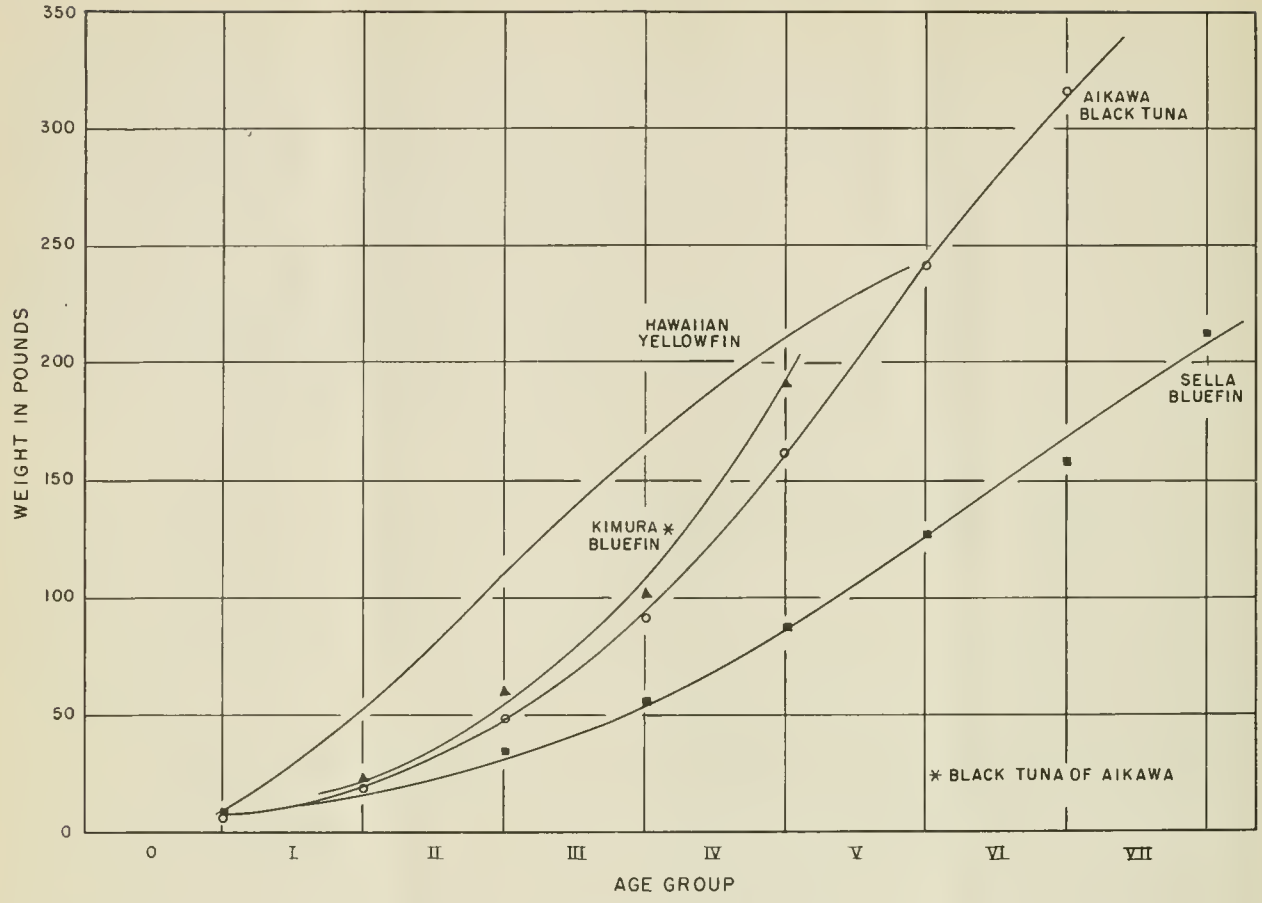

FIGURE 13.—Age-weight curves of tunas from waters off Japan and Mediterranean Sea compared to curve of Hawaiian yellowfin.

demonstrates the most rapid growth but shows no semblance of a point of inflection. As the curves have been fitted to the data by eye, there may be errors in the interpretation, but the curves show the great variation in results of age and growth studies of tunas.

Westman and Neville (1942), in a study of 751 length frequencies of bluefin tuna (*Thunnus thynnus*) taken in waters off New York by both the troll and chum fisheries, show the catch to be made up of three distinct age groups. Ages were assigned by scale readings. A comparison of size of fish by ages with the Hawaiian-yellowfin study shows more similarity than the curves indicate in figure 13. Even so, the growth rate of the Atlantic bluefin as shown by plotted data (fig. 14) is not so rapid as yellowfin growth during the early years of life.

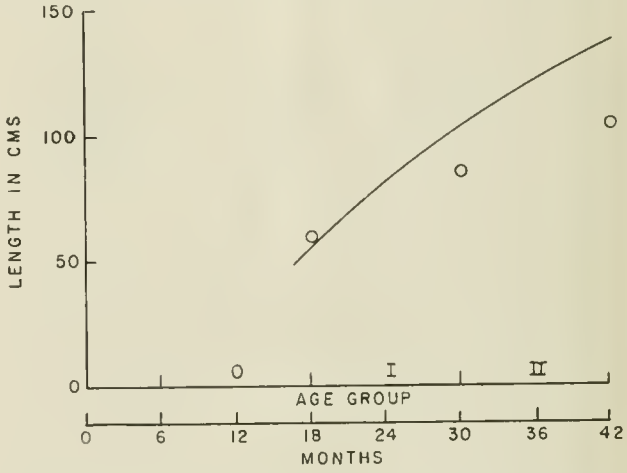

FIGURE 14.—Lengths of dominant size groups of bluefin tuna taken off Long Island, New York, by Westman and Neville (1942), plotted against the calculated growth curve of Hawaiian yellowfin.

In general, the results of our study of weight frequencies of Hawaiian yellowfin tend to disagree with results of some studies of other species of tuna and even with comparable yellowfin studies. Group *N*, present in the Hawaiian long-line catches of both 1948 and 1949, is with little doubt an age group demonstrating a weight gain of about 60 pounds in the calendar year. Whether or not our conclusions about age are correct in other respects, the yellowfin tuna of Hawaiian waters undoubtedly is a rapid-growing species.

CONCLUSIONS

1. The yellowfin tuna (*Neothunnus macropterus*) in Hawaiian waters is a rapid-growing fish demonstrating at least during part of its life a growth of approximately 60 pounds in one calendar year.

2. Positions of modes of size frequencies are well fitted by a growth curve calculated by Walford's graphic transformation method, having an upper asymptote at 294.9 pounds.

3. Extrapolation of the calculated curve downward shows the spawning period in reference to mode *N* to be in year *N*—III. If this interpretation is valid, mode *N* is composed of fish which were completing their third year of life and entering their fourth in the middle of the calendar year of observation.

Using the customary designation of age groups according to completed years of life, they would be designated age group II until the middle of the spawning season which occurs in the middle of the calendar year, and then become age group III.

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APPENDIX

The following tables of data on yellowfin tuna are those on which the figures and calculations in the text are based.

TABLE A.—*Weight frequencies of yellowfin tuna taken by long-line fishing and landed at Honolulu during November and December 1947*

Class interval	November	December	Number of tuna landed
70 to 79 pounds		2	2
80 to 89 pounds	1	1	2
90 to 99 pounds		2	2
100 to 109 pounds	2		2
110 to 119 pounds	1	2	3
120 to 129 pounds	1	5	6
130 to 139 pounds	3	9	12
140 to 149 pounds	4	9	13
150 to 159 pounds		10	10
160 to 169 pounds	4	14	18
170 to 179 pounds	9	11	20
180 to 189 pounds	7	10	17
190 to 199 pounds	1	5	6
200 to 209 pounds	6	3	9
210 to 219 pounds	2	3	5
220 to 229 pounds	2		2
230 to 239 pounds	1	2	3
240 to 249 pounds			
250 to 259 pounds			
260 to 269 pounds	1		1
Total	45	88	133

TABLE B.—*Weight frequencies of yellowfin tuna taken by long-line fishing and landed at Honolulu during 1948*

Class interval	January	February	March	April	May	June	July	August	September	October	November	December	Number of tuna landed
20 to 29 pounds												1	1
30 to 39 pounds												1	1
40 to 49 pounds			1							3		2	6
50 to 59 pounds			1		1				1		1	2	6
60 to 69 pounds	1	1		1				2	5	4	2	5	21
70 to 79 pounds	7	3	2	1	2		1		2	4	3	6	31
80 to 89 pounds	4	8	4		3	6	3	3	2	1	2	9	45
90 to 99 pounds	2	4	7	1	8	13	16	10	6	7	3	2	79
100 to 109 pounds	4	3	3	9	19	54	80	41	31	20	3	1	268
110 to 119 pounds	1	2	4	3	15	68	90	71	55	34	10	8	361
120 to 129 pounds	4	3	1	11	9	45	60	59	45	24	8	3	272
130 to 139 pounds	1	6	4	8	6	29	25	53	39	18	18	11	218
140 to 149 pounds	1	5	6	8	3	30	40	46	25	17	10	8	199
150 to 159 pounds	4	8	5	7	8	24	30	49	37	11	8	7	198
160 to 169 pounds	3	6	4	4	9	24	51	49	44	12	5	5	216
170 to 179 pounds	3	5		3	3	24	34	40	19	5	6	5	147
180 to 189 pounds	3	2	1	2	1	9	29	46	25	8	10	6	142
190 to 199 pounds	1	4	1	2	2	13	30	37	19	7	4	5	125
200 to 209 pounds	1	1			4	17	18	21	16	1	2	4	85
210 to 219 pounds					3	3	15	11	8	3	2	1	46
220 to 229 pounds			1			3	3	3					10
230 to 239 pounds							2		2				4
240 to 249 pounds							2	1			1		4
250 to 259 pounds							1				1		2
260 to 269 pounds					1								1
Total	40	61	45	60	97	362	530	542	381	179	99	92	2,488

TABLE C.—*Weight frequencies of yellowfin tuna taken by long-line fishing and landed at Honolulu, 1949*

Class interval	January	February	March	April	May	June	July	August	September	October	November	December	Number of tuna landed
20 to 29 pounds	1												1
30 to 39 pounds		1											1
40 to 49 pounds				1								1	2
50 to 59 pounds	1	1				1	1	2					6
60 to 69 pounds	4	2	1		3							4	14
70 to 79 pounds	12	7	2		1		1		1	4		2	30
80 to 89 pounds	5	15	2	2	2	2	3	4	6	6		10	57
90 to 99 pounds		7	5	9	24	20	16	7	2	8	2	9	109
100 to 109 pounds	2	4	1	11	23	62	52	39	10	4	2	7	217
110 to 119 pounds	1	1	1	8	11	51	77	58	23	10	2	6	249
120 to 129 pounds	1	4		14	16	52	68	37	23	11	9	3	238
130 to 139 pounds	4	8	3	9	20	60	65	46	19	12	1	4	251
140 to 149 pounds	1	3	1	4	18	56	42	39	12	10	1	4	191
150 to 159 pounds	1	6	3	1	7	63	51	37	16	7	3	4	199
160 to 169 pounds	2	5		2	12	43	47	31	12	7	1	3	165
170 to 179 pounds	2	5		4	5	33	42	30	9	6	4	4	144
180 to 189 pounds		3	1	1	4	15	28	17	8	3	1	3	84
190 to 199 pounds				1	2	17	17	20	5	6		2	70
200 to 209 pounds	1				5	18	21	20	13	2	2		82
210 to 219 pounds		1			3	13	9	10	4	4		1	45
220 to 229 pounds					2	5	4	2	2	1	1		17
230 to 239 pounds						3	1	1			1		6
240 to 249 pounds	1										1		2
250 to 259 pounds										1			1
260 to 269 pounds													
Total	39	73	20	67	158	514	545	400	165	102	31	67	2,181

TABLE D.—*Weight frequencies of yellowfin tuna taken by long-line fishing and landed at Honolulu, 1948 and 1949 combined*

Class interval	January	February	March	April	May	June	July	August	September	October	November	December	Number of tuna landed
20 to 29 pounds	1											1	2
30 to 39 pounds		1										1	2
40 to 49 pounds			1	1						3		3	8
50 to 59 pounds	1	1	1		1	1	1	2	1		1	2	12
60 to 69 pounds	5	3	1	1	3			2	5	4	2	9	35
70 to 79 pounds	19	10	4	1	3		2		3	8	3	8	61
80 to 89 pounds	9	23	6	2	5	8	6	7	8	7	2	19	102
90 to 99 pounds	2	11	12	10	32	33	32	17	8	15	5	11	188
100 to 109	6	7	4	20	42	116	132	80	41	24	5	8	485
110 to 119 pounds	2	3	5	11	26	119	167	129	78	44	12	14	610
120 to 129 pounds	5	7	1	25	25	97	128	96	68	35	17	6	510
130 to 139 pounds	5	14	7	17	26	89	90	99	58	30	19	15	469
140 to 149 pounds	2	8	7	12	21	86	82	85	37	27	11	12	390
150 to 159 pounds	5	14	8	8	15	87	81	86	53	18	11	11	397
160 to 169 pounds	5	11	4	6	21	67	98	80	56	19	6	8	381
170 to 179 pounds	5	10		7	8	57	76	70	28	11	10	9	291
180 to 189 pounds	3	5	2	3	5	24	57	63	33	11	11	9	226
190 to 199 pounds	1	4	1	3	4	30	47	57	24	13	4	7	195
200 to 209 pounds	2	1			9	35	39	41	29	3	4	4	167
210 to 219 pounds		1			6	16	24	21	12	7	2	2	91
220 to 229 pounds			1		2	8	7	5	2	1	1		27
230 to 239 pounds						3	3	1	2		1		10
240 to 249 pounds	1						2	1			2		6
250 to 259 pounds							1			1	1		3
260 to 269 pounds					1								1
Total	79	134	65	127	255	876	1,075	942	546	281	130	159	4,669

TABLE E.—*Weight frequencies of yellowfin tuna taken by live-bait fishing and trolling and landed at Honolulu during 1949*

Class interval	January	February	March	April	May	June	July	August	September	October	November	December	Number of tuna landed
0 to 9 pounds					22	54							76
10 to 19 pounds	6	3			1	1		1					12
20 to 29 pounds	1		1	1	1								4
30 to 39 pounds				13	15	2	1	1					32
Total	7	3	1	14	39	57	1	2					124

TABLE F.—*Weight frequencies of yellowfin tuna taken by long-line and live-bait fishing and landed at Honolulu during 1948 and 1949*

Class interval	January	February	March	April	May	June	July	August	September	October	November	December	Number of tuna landed
0 to 9 pounds					22	54							76
10 to 19 pounds	6	3			1	1		1					12
20 to 29 pounds	2		1	1	1							1	6
30 to 39 pounds		1		13	15	2	1	1				1	34
40 to 49 pounds			1	1						3		3	8
50 to 59 pounds	1	1	1		1	1	1	2	1		1	2	12
60 to 69 pounds	5	3	1	1	3			2	5	4	2	9	35
70 to 79 pounds	19	10	4	1	3		2		3	8	3	8	61
80 to 90 pounds	9	23	6	2	5	8	6	7	8	7	2	19	102
90 to 99 pounds	2	11	12	10	32	33	32	17	8	15	5	11	188
100 to 109 pounds	6	7	4	20	42	116	132	80	41	24	5	8	485
110 to 119 pounds	2	3	5	11	26	119	167	129	78	44	12	14	610
120 to 129 pounds	5	7	1	25	25	97	128	96	68	35	17	6	510
130 to 139 pounds	5	14	7	17	26	89	90	99	58	30	19	15	469
140 to 149 pounds	2	8	7	12	21	86	82	85	37	27	11	12	390
150 to 159 pounds	5	14	8	8	15	87	81	86	53	18	11	11	397
160 to 169 pounds	5	11	4	6	21	67	98	80	56	19	6	8	381
170 to 179 pounds	5	10		7	8	57	76	70	28	11	10	9	291
180 to 189 pounds	3	5	2	3	5	24	57	63	33	11	11	9	226
190 to 199 pounds	1	4	1	3	4	30	47	57	24	13	4	7	195
200 to 209 pounds	2	1			9	35	39	41	29	3	4	4	167
210 to 219 pounds		1			6	16	24	21	12	7	2	2	91
220 to 229 pounds			1		2	8	7	5	2	1	1		27
230 to 239 pounds						3	3	1	2		1		10
240 to 249 pounds	1						2	1			2		6
250 to 259 pounds							1			1	1		3
260 to 269 pounds					1								1
Total	86	137	66	141	294	933	1,076	944	546	281	130	159	4,793

TABLE G.—*Weight frequencies of yellowfin tuna taken by long-line and live-bait fishing during 1948 and 1949 as percentages of monthly catch with mean frequency distribution in percentage*

Class interval	January	February	March	April	May	June	July	August	September	October	November	December	Mean
0 to 9 pounds					7.5	5.8							1.1
10 to 19 pounds	7.0	2.2			0.3	0.1		0.1					0.8
20 to 29 pounds	2.3		1.5	0.7	0.3							0.6	0.4
30 to 39 pounds		0.7		9.2	5.1	0.2	0.1	0.1				0.6	1.3
40 to 49 pounds			1.5	0.7						1.1		1.9	0.4
50 to 59 pounds	1.2	0.7	1.5		0.3	0.1	0.1	0.2	0.2		0.8	1.3	0.5
60 to 69 pounds	5.8	2.2	1.5	0.7	1.0			0.2	0.9	1.4	1.5	5.7	1.7
70 to 79 pounds	22.1	7.3	6.1	0.7	1.0		0.2		0.6	2.8	2.3	5.0	4.0
80 to 89 pounds	10.5	16.8	9.1	1.4	2.6	0.8	0.6	0.7	1.5	2.5	1.5	11.9	5.0
90 to 99 pounds	2.3	8.0	18.2	7.1	10.9	3.5	3.0	1.8	1.5	5.3	3.8	6.9	6.0
100 to 109 pounds	7.0	5.1	6.1	14.2	14.3	12.4	12.3	8.5	7.5	8.5	3.8	5.0	8.7
110 to 119 pounds	2.3	2.2	7.6	7.8	8.8	12.8	15.5	13.7	14.3	15.7	9.2	8.8	9.9
120 to 129 pounds	5.8	5.1	1.5	17.7	8.5	10.4	11.9	10.2	12.4	12.5	13.1	3.8	9.4
130 to 139 pounds	5.8	10.2	10.6	12.0	8.8	9.5	8.4	10.5	10.6	10.7	14.6	9.4	10.1
140 to 149 pounds	2.3	5.8	10.6	8.5	7.1	9.2	7.6	9.0	6.8	9.6	8.5	7.6	7.7
150 to 159 pounds	5.8	10.2	12.1	5.7	5.1	9.3	7.5	9.1	9.7	6.4	8.5	6.9	8.0
160 to 169 pounds	5.8	8.0	6.1	4.2	7.1	7.2	9.1	8.5	10.3	6.8	4.6	5.0	6.9
170 to 179 pounds	5.8	7.3		5.0	2.7	6.1	7.1	7.4	5.1	3.9	7.7	5.7	5.3
180 to 189 pounds	3.5	3.6	3.0	2.1	2.6	2.6	5.3	6.7	6.0	3.9	8.5	5.7	4.4
190 to 199 pounds	1.2	2.9	1.5	2.1	1.4	3.2	4.4	6.0	4.4	4.6	3.1	4.4	3.3
200 to 209 pounds	2.3	0.7			3.1	3.8	3.6	4.3	5.3	1.1	3.1	2.5	2.5
210 to 219 pounds		0.7			2.0	1.7	2.2	2.2	2.2	2.5	1.5	1.3	1.4
220 to 229 pounds			1.5		0.7	0.8	0.6	0.5	0.4	0.4	0.8		0.5
230 to 239 pounds						0.3	0.3	0.1	0.4		0.8		0.2
240 to 249 pounds	1.2						0.2	0.1			.5		0.2
250 to 259 pounds							0.1			0.4	0.8		0.1
260 to 269 pounds					0.3								

TABLE H.—*Time and position of recognized and interpolated modes from the combined 1948 and 1949 data*

Month	Number	Observed length, in centimeters	Interpolated length, in centimeters
May	17	47.2	
June	18	47.2	
July	19		50.4
August	20		53.6
September	21		56.8
October	22		60.0
November	23		63.2
December	24		66.5
January	25	69.7	
February	26		77.5
March	27		85.2
April	28	93.0	
May	29	93.0	
June	30		97.6
July	31		102.2
August	32		106.8
September	33		111.4
October	34		116.0
November	35		120.7
December	36	125.3	
January	37	120.2	
February	38	125.3	
March	39	130.1	
April	40	142.6	
May	41	134.5	
June	42	138.7	
July	43	138.7	
August	44	138.7	
September	45	140.3	
October	46	138.7	
November	47	146.3	
December	48		149.7
January	49		153.0
February	50	156.4	
March	51	152.1	
April	52		152.2
May	53		152.3
June	54	152.4	
July	55	158.2	
August	56		157.3
September	57	156.4	
October	58		159.4
November	59	162.5	
December	60	163.1	
January	61		163.6
February	62		164.1
March	63		164.6
April	64		165.1
May	65		165.6
June	66		166.1
July	67		166.6
August	68		167.1
September	69	167.6	

UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*

FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

STUDIES OF GEORGES BANK HADDOCK

Part I: Landings by Pounds, Numbers, and Sizes of Fish

By Howard A. Schuck

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CONTENTS

	Page
Introduction	151
Fishing banks and areas studied	152
Organization of study	153
Development of data	153
Ports of landing	153
Categories of fish	156
Seasons	157
Segregating landings by subareas	157
Pounds of haddock landed	157
Average weights of haddock landed	159
Numbers of haddock landed	162
Size compositions of haddock landed	162
Scrod haddock	164
Large haddock	164
Total haddock	164
Undersized haddock	166
Scrod versus large haddock	166
Discussion and summary	174
Literature cited	176

STUDIES OF GEORGES BANK HADDOCK

Part I: Landings by Pounds, Numbers, and Sizes of Fish

By HOWARD A. SCHUCK, *Fishery Research Biologist*

The haddock, *Melanogrammus aeglefinus*, has been New England's most valuable fishery resource, and one of the most important in the United States, for nearly three decades. In the early days, this fish was little sought and the annual New England catch was small—only about 40-odd million pounds until well into the 1900's. With the development of filleting and freezing methods the market for haddock grew, and during the 1920's New England landings increased greatly. They reached a peak of about 250 million pounds in 1929, but after that production declined rapidly.

From Georges Bank, source of most United States haddock, production dropped from about 223 million pounds in 1929 to 115 million pounds in 1931. In addition, an index of abundance indicates that the size of the stock on Georges Bank declined greatly over these years.

The decline of haddock landings and abundance aroused concern in the fishing industry, and in 1930 funds were made available to the United States Bureau of Fisheries (now the Fish and Wildlife Service) to study the haddock and the haddock fishery. The general purposes of the investigation were to determine (1) what caused the decline of the fishery in waters fished by United States fishermen, (2) what could be done to increase abundance and production, or at least to prevent them from decreasing further, and (3) what predictions of future production were possible.

During the years 1931–48, a large quantity of data was collected, partly at sea but mostly at the important haddock ports (Boston, Gloucester, and New Bedford, Mass., and Portland, Maine) where collectors and interviewers have worked systematically since 1931. These data, the basis of this and other papers, were obtained with the cooperation of fishermen at sea and of boat owners, dealers, and fish handlers—especially those on the Boston Fish Pier (fig. 1).

William C. Herrington, in charge of the Haddock Investigation from 1931 to 1947, planned the collection of these data obtained in various years during the period 1931–48 by many employees of the Fish and Wildlife Service. Among these were H. M. Bearse, F. E. Firth, D. F. Hammack, J. J. Miggins, J. M. Shuval, and J. R. Webster. Assisting in tabulating and summarizing data at various times during the years 1945–49 were E. L. Arnold, Jr., F. A. Dreyer, Dorothy B. Monahan, Elizabeth V. Nugent, E. S. Phillips, S. L. Cogswell, and L. D. Stringer.

At sea, data were collected on commercial fishing vessels; on the *Atlantis*, a research vessel leased from the Woods Hole Oceanographic Institution; and on the fishery-research vessels *Albatross II* (1931 and 1932) and *Albatross III* (beginning in 1948). Most of these data were collected to determine how to protect small haddock, destroyed in large numbers by the otter-trawl (fig. 2) fleet. Line trawlers (fig. 3) were used in the early days of the haddock fishery, but now only two are operating out of Boston, Mass., the major haddock port. Results of these studies on the small haddock situation were reported by Herrington (1933, 1935, 1936, 1941).[1] In addition, a small amount of tagging was done to determine migrations and interdependence of populations. Most of this work remains unreported, but one publication refers to phases of it (Rounsefell 1942). And since the commissioning of the *Albatross III* in 1948, further experiments on mesh sizes, studies of survival of young haddock that escape through larger mesh, some tagging, and a census of the population of all ages of haddock have been undertaken.

At the important haddock ports considerable quantities of data were obtained. These data are largely unreported, although contributions of Herrington (1944, 1948) and Schuck (1949) have presented segments of them and certain conclu-

[1] Publications referred to parenthetically by date are listed in the Literature Cited, p. 176.

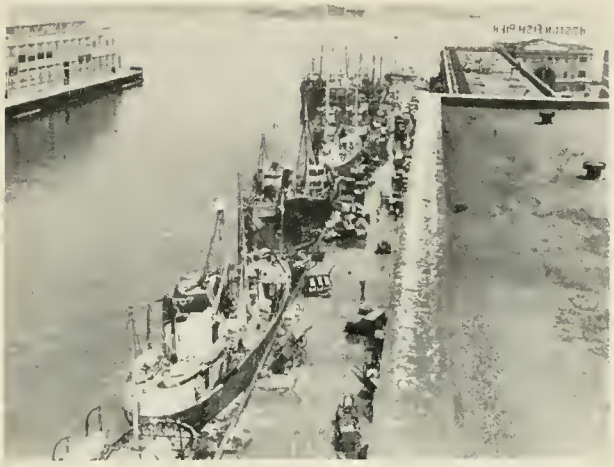

FIGURE 1.—Part of the Boston Fish Pier, where most of the United States production of haddock is landed.

FIGURE 2.—Modern otter trawler: predominant type of vessel in the present-day New England haddock fishery.

FIGURE 3.—Line trawler: predominant type of vessel in the early years of the New England haddock fishery.

sions regarding the fishery. At the ports, since 1931, the following data have been collected: (1) Almost complete records of the poundages landed from various banks, with records of depths and locations from which the fish were taken, the gear used, and the days actually spent fishing; (2) randomized samples of the lengths of fish in the landings; (3) selected samples of scales; and (4) length-weight data.

FISHING BANKS AND AREAS STUDIED

The United States haddock fishery has depended upon Georges Bank and the Nova Scotian banks. To the north of these banks, haddock are found, but are little fished by United States fishermen. To the south, haddock are not found, except for stragglers.

Georges Bank is the most important area for the United States haddock fishery, with about 67 percent of the total United States landings coming from this area during recent years (1931 to 1948).

The haddock on Georges Bank are apparently a relatively distinct and homogeneous stock. Present knowledge indicates that the Fundian Channel, which separates Georges Bank from the Nova Scotian banks, is a natural barrier to the intermigration of bottom-living stages of haddock. Evidence of this comes from studies of size compositions, growth rates, tagging, and vertebral counts. The size composition of the stock and the sizes of haddock of various ages on Georges Bank are decidedly different from those on Browns Bank across the Fundian Channel (Needler 1930, Schuck and Arnold in press). Although the number of tagged haddock is not large, there is no evidence from the returns that any of them crossed this channel (Needler 1930, Schroeder 1942, United States Fish and Wildlife Service unpublished data). There is a seasonal migration in the spring from Georges Bank north along the coast of Massachusetts and Maine as far as the Bay of Fundy and a return to Georges Bank in the fall, but very few haddock are caught on this northward migration.

Because, first, the Georges Bank area was the most important for the United States haddock fishery and, second, the haddock on Georges Bank formed a relatively distinct population and, third, haddock production from this bank had declined more seriously than production from the Nova Scotian banks, we decided to study first the

Georges Bank haddock—before the Nova Scotian haddock.

The Georges Bank region comprises most of International Area XXII, shown in figure 4. International Area XXII was established by the North American Council on Fishery Investigation when the western North Atlantic Ocean was divided along natural, political, and ecological lines. By Georges Bank we mean specifically the following subareas (fig. 5) of Area XXII:

	International subarea
1. Northern Edge and Northeast Peak	J
2. Southeast Part of Georges	M
3. Southwest Georges	N
4. South Channel and Nantucket Shoals	G, H, O [1]

[1] Data include very small quantities from subareas Q, R, and S.

The manner by which these subareas were established is described by Rounsefell (1948).

ORGANIZATION OF STUDY

Russell (1942) has expressed the dynamics of a fish population by the equation

$$S_1+(G+R)-(C+N)=S_2$$

where

S_1=size of population at the beginning of the year,

G=additions to the population during the year by growth,

R=additions to the population by recruitment of young fish,

C=deductions from the population during the year by fishery,

N=deductions from the population during the year due to natural mortality,

S_2=size of population at the end of the year.

The main problems, as we see them, are (1) to obtain accurate measures of the various quantities expressed in this equation for each year, (2) to determine what effect variations of catch, natural mortality, growth, and recruitment have had on the size of the stock, (3) to determine what effect variations in the size of the stock have had upon each of these factors, and (4) to show what effect other factors in the environment (hydrographic conditions and stocks of other species of competing fishes) have had upon (*a*) the size of the stock and (*b*) the four factors—catch, growth, recruitment, and natural mortality.

With this information at hand, if the relative effects of the fishery and of the environment on the stock are sufficiently clear, it should be possible (1) to predict the abundance and production of haddock, and (2) to determine what measures, if any, would maintain or increase the catch of haddock from the important populations.

Most of the material in this series is devoted to solving these problems. The purpose of the remainder of the present paper is restricted to determining the total landings of Georges Bank haddock for each season and year, 1931 to 1948, in terms of pounds, numbers, average weights, and numbers of each size.

Obtaining "total" values implies adding together not only those portions of the landings of the various ports that originated on Georges Bank, but adding together also data for two artificial market categories, the limits of which vary from season to season, from year to year, and among different areas of the bank.

Where we refer to totals we refer, of course, to our best estimate of such values. All such values are subject to a certain amount of error due to limitations in collecting and assembling statistics and to sampling error.

The values developed in this paper represent landings but not catches because the smallest sizes of haddock are discarded at sea as they lack sufficient marketable value to be brought to port.

DEVELOPMENT OF DATA

Ports of landing

Haddock are caught in North American waters by fishermen from New England, New York, Canada, Newfoundland, and various European countries.

Canadian and Newfoundland landings were excluded from this study, as no records could be found to indicate that any of their haddock were caught in the Georges Bank area. McKenzie (1946) has shown that all Canadian haddock landings for the years 1938 to 1940 came from banks to the north and east of Georges Bank. Herrington (unpublished manuscript) lists all Canadian landings for the years 1918 to 1940 as having originated from banks other than Georges.

European fishermen, mainly interested in cod, frequent the Newfoundland banks and the most easterly of the Nova Scotian banks. Records show that Europeans fished on Georges Bank during early years, but not during the years covered in this summary.

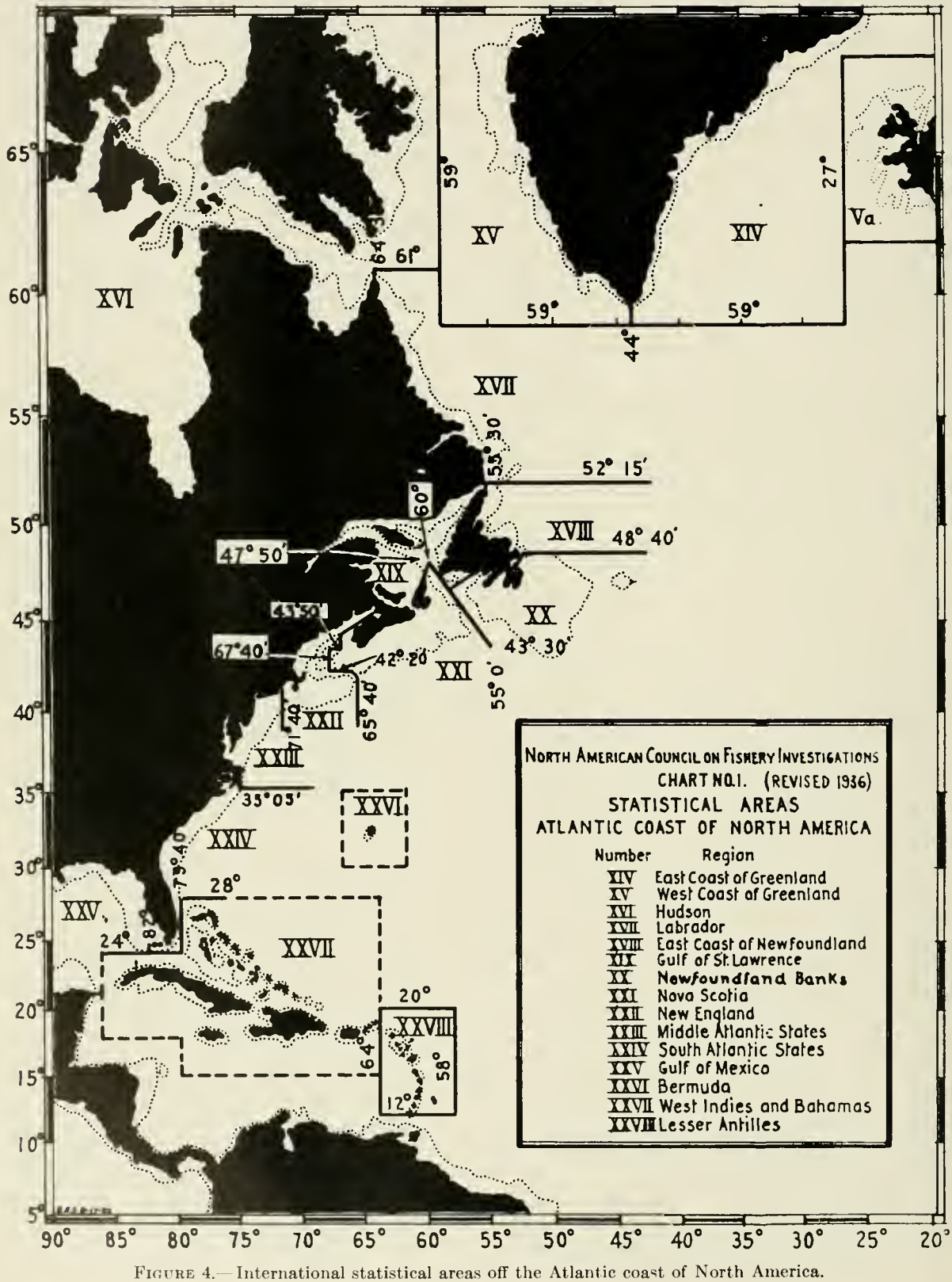

FIGURE 4.—International statistical areas off the Atlantic coast of North America.

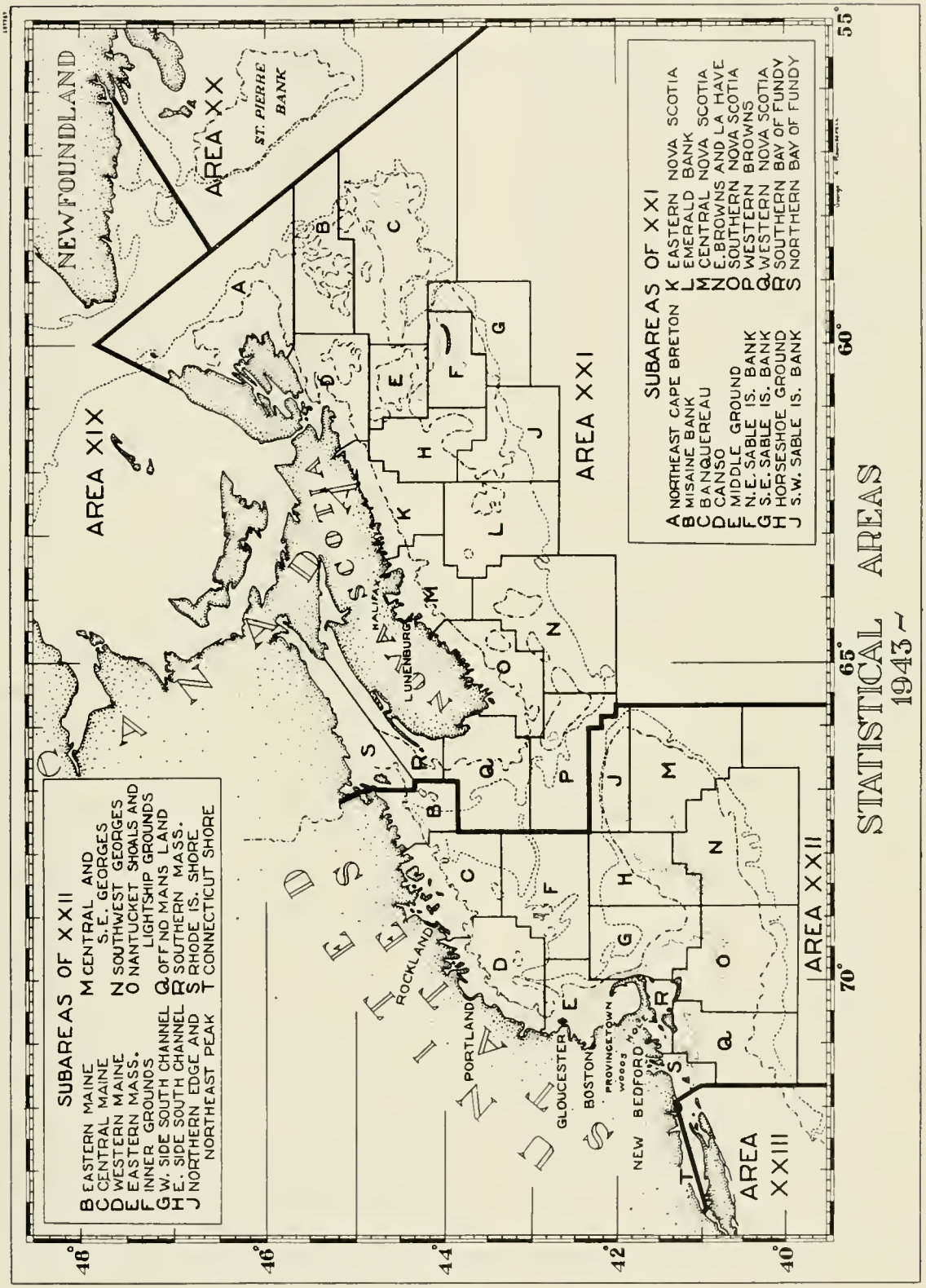

FIGURE 5.—Subareas currently used in International Areas XXI and XXII.

Thus United States fishermen were the only ones to land haddock from Georges Bank. However, we could not use the total of all United States landings of haddock for this study because United States fishermen took varying quantities of haddock from other banks as well as from Georges.

Inasmuch as Georges Bank lies at a considerable distance off shore, it is exploited mainly by large vessels. These vessels land at only a few ports where, for the most part, accurate records have been kept on the origin of haddock landings. Thus for Boston and Gloucester we were able to determine the quantities of haddock landed from Georges Bank each year. We included also in our tabulations the quantities of Georges Bank haddock landed at Portland, Maine, during the years 1931 to 1946. And beginning in 1942, landings of haddock at the port of New Bedford became quite large, so the New Bedford landings of Georges Bank haddock for the years 1942 to 1948 were included. As almost all haddock landed at New York City are taken from the Georges area, the total of that port's landings for all years also were included. We included also the total landings for Groton, Conn. for 1931 and 1932—landings at this port were negligible after 1932. To these quantities, we added the entire amount of haddock landed on Cape Cod, which lies next to Georges Bank. This is the only area where small boats land Georges Bank haddock, and almost all landings there are from Georges.

The sums of these quantities we have accepted as the total poundages [2] of haddock originating in the Georges area that were landed and sold.

Categories of fish

Immediately after capture at sea, haddock are separated into two market categories, scrod and large. This division of the catch makes it necessary to collect complete data on each market category and later to combine the data to obtain total statistics for the species haddock.

As defined by the New England Fish Exchange, scrod haddock (scrod) are those weighing from 1½ to 2½ pounds (gutted weight), and large haddock are those weighing more than 2½ pounds. These definitions are only approximate owing to variations in culling and to a practice of marketing, as scrod, many fish weighing less than 1½ pounds.

We have tabulated records of the landings for both market categories, large and scrod, for all years. Small amounts of "mixed" haddock were added to scrod in New Bedford. When OPA price control regulations were in effect (which allowed a higher price for "large" haddock), New Bedford landings showed an artificial scarcity of scrod and an overabundance of large. For the period July 1943 to June 1946, therefore, we used the percentage that scrod made up of the monthly total of scrod and large for the ports of Boston, Gloucester, and Portland, from any subarea in any month, to estimate the proportion of scrod in the New Bedford landings from these same subareas in that month.

Where we refer to "undersized" haddock we mean those less than 1½ pounds, the lower limit of the market category of scrod, although at present there is no State or Federal regulation that classifies such fish as undersized. When we refer to "total haddock" or merely "haddock", we mean the total of all haddock regardless of market category.

Most haddock are landed as drawn or gutted fish, but some are landed in the "round". Where poundages of fish in the round were obtained, they were reduced by 15 percent. Thus all poundages are in terms of gutted fish.

Landings of large haddock in the round were negligible but landings of round scrod were more numerous and were of two types, (1) regular-sized scrod that were left ungutted because of rough weather or gluts of fish on deck, and (2) unusually small-sized scrod, or baby scrod. Landings of baby scrod became unusually large in the winter of 1940, owing to a scarcity of large haddock and a high abundance of baby haddock (year class 1939).

The landings of baby scrod from the winter of 1940 to the summer of 1943 were considered to be so large that in the initial steps of the analysis they were treated separately from scrod or large haddock. These landings of baby scrod amounted to approximately the following:

[2] Sources of data are the former U. S. Bureau of Fisheries and the present U. S. Fish and Wildlife Service publications, "Current Fishery Statistics" for all years, and unpublished records of various fish companies assembled by William C. Herrington.

	Thousands of pounds
Year 1940:	
Fall	33
Winter	1,097
Year 1941:	
Spring	3,153
Summer	1,683
Fall	913
Winter	339
Year 1942:	
Spring	239
Summer	380
Fall	275
Winter	362
Year 1943:	
Spring	2,212
Summer	429
Fall	25

Seasons

A "haddock year" is the summation of spring, summer, fall, and winter seasons, and differs from a calendar year by one month. These seasons are as follows:

	Months
Spring	February, March, April.
Summer	May, June, July.
Fall	August, September, October.
Winter	November, December, January (of following year).

These seasons agree with the Georges Bank haddock life-cycle better than any other 3-month grouping, for the months of February, March, and April constitute the spawning period. During these months the size and age composition of the catch is considerably different from that of each of the other seasons.

All data were collected initially on a monthly basis, then assembled into seasons, and then into haddock years.

Segregating landings by subareas

Inasmuch as different sizes of haddock are caught on various parts of Georges Bank, we wished in the initial steps of development of the data to segregate the landings by subareas. For the ports of Boston, Gloucester, New Bedford, and Portland, accurate information was obtained on the amounts of haddock landed from each subarea. These ports received the bulk of the total landings (88 percent for all years), thus we allotted the remainder of the landings to subareas on the basis of the subarea contribution at these ports.

The subareas shown in figure 5 were in use from 1939 through 1948. In the years before 1939, there were several different systems of naming and segregating the various sections of Georges Bank. The data from earlier years, therefore, were arranged to conform, as much as possible, to the modern subareas. One exception should be noted, however. During the years 1931 through 1935, published statistics furnished a breakdown by only (1) South Channel and Nantucket Shoals, and (2) the rest of Georges Bank proper—roughly J, M, and N of the modern terminology.

In all tables showing pounds and numbers of fish, values were rounded off to the nearest thousand. Total as well as individual values were rounded off. Thus, individual values do not add up exactly to the totals in some cases.

POUNDS OF HADDOCK LANDED

Table 1 shows the pounds of scrod and large haddock landed from the four subareas of Georges Bank by seasons and years, from 1931 through 1948. Whether particular subareas of Georges Bank contributed more or less haddock in recent years can be studied through this table. Their importance, relative to one another, is shown in table 2 (percent contribution by years, 1936–48 only). The landings are summarized, by seasons, for scrod in table 3, for large in table 4, and for total haddock in table 5. Landings by years only are shown also in tables 3, 4, and 5, and in figure 6.

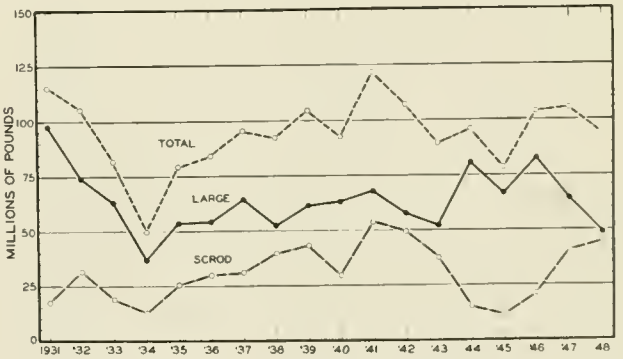

FIGURE 6.—Pounds of scrod, large, and total haddock landed from Georges Bank, 1931 to 1948.

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TABLE 1.—*Scrod and large haddock landed, by subareas and by seasons, 1931 to 1948*

[In thousands of pounds]

Season	Scrod				Large			
	Northern Edge	Southeast Part	Southwest Part	South Channel	Northern Edge	Southeast Part	Southwest Part	South Channel
Year 1931:								
Spring		[1] 705		189		[1] 24,400		5,211
Summer		[1] 850		405		[1] 18,822		14,788
Fall		[1] 3,997		1,269		[1] 13,629		10,198
Winter		[1] 8,613		1,473		[1] 7,637		2,854
Year 1932:								
Spring		[1] 4,702		2,253		[1] 8,850		9,286
Summer		[1] 6,797		1,940		[1] 14,006		5,528
Fall		[1] 10,808		991		[1] 16,126		7,177
Winter		[1] 3,226		796		[1] 8,420		4,514
Year 1933:								
Spring		[1] 3,441		675		[1] 14,455		3,912
Summer		[1] 3,010		1,510		[1] 12,056		8,659
Fall		[1] 7,725		906		[1] 14,465		5,030
Winter		[1] 1,245		286		[1] 2,542		1,723
Year 1934:								
Spring		[1] 888		717		[1] 4,190		3,071
Summer		[1] 2,525		963		[1] 7,535		6,418
Fall		[1] 5,042		996		[1] 7,872		4,908
Winter		[1] 1,655		190		[1] 2,413		501
Year 1935:								
Spring		[1] 769		194		[1] 4,345		821
Summer		[1] 4,802		915		[1] 14,861		3,762
Fall		[1] 9,509		1,045		[1] 13,639		4,402
Winter		[1] 8,037		266		[1] 11,082		732
Total, 1931–35:								
Spring		[1] 10,505		4,028		[1] 56,240		22,301
Summer		[1] 17,984		5,733		[1] 67,280		39,155
Fall		[1] 37,081		5,207		[1] 65,731		31,715
Winter		[1] 22,776		3,011		[1] 32,094		10,324
Year 1936:								
Spring	2,478	875	31	488	7,620	3,664	235	2,309
Summer	3,438	4,235	375	1,556	6,440	5,475	293	5,010
Fall	11,368	1,216	0	349	13,382	883	0	2,094
Winter	1,045	1,816	96	584	1,892	2,425	213	2,133
Year 1937:								
Spring	4,489	816	11	198	15,665	2,562	158	1,320
Summer	5,476	1,204	185	1,558	9,326	2,109	506	5,490
Fall	10,207	1,246	44	3,168	10,147	706	18	6,776
Winter	1,114	536	35	797	3,346	1,055	125	5,062
Year 1938:								
Spring	1,680	1,662	151	814	5,853	5,670	566	3,194
Summer	5,260	966	32	1,724	8,162	1,721	156	5,598
Fall	13,086	1,306	20	6,002	6,404	539	13	5,878
Winter	2,313	2,485	173	2,233	2,173	2,077	314	4,162
Year 1939:								
Spring	993	3,611	181	2,739	2,609	7,747	364	5,091
Summer	4,298	2,900	458	4,087	6,831	3,841	978	6,468
Fall	8,592	1,081	0	8,043	8,758	834	0	7,784
Winter	1,843	1,682	295	2,322	2,617	2,294	283	4,911

[1] Pounds shown for 1931 to 1935 are combined for Northern Edge, Southeast Part, and Southwest Edge.

TABLE 1.—*Scrod and large haddock landed, by subareas and by seasons, 1931 to 1948*—Continued

[In thousands of pounds]

Season	Scrod				Large			
	Northern Edge	Southeast Part	Southwest Part	South Channel	Northern Edge	Southeast Part	Southwest Part	South Channel
Year 1940:								
Spring	2,156	1,429	7	3,022	4,634	4,713	63	6,353
Summer	3,165	2,508	639	3,081	6,417	6,062	1,998	7,727
Fall	4,535	1,407	28	3,537	8,146	1,797	33	6,514
Winter	176	1,271	1,532	1,107	498	2,508	2,010	3,572
Year 1941:								
Spring	1,916	4,042	883	4,773	2,597	12,139	866	4,072
Summer	2,200	4,698	1,697	4,983	4,380	7,619	2,738	9,071
Fall	8,553	6,151	421	5,941	7,055	2,602	287	6,017
Winter	210	3,318	1,636	2,342	264	2,343	1,397	4,515
Year 1942:								
Spring	3,445	4,892	138	3,009	3,745	9,531	456	3,138
Summer	8,462	3,780	630	4,154	8,221	4,202	914	6,963
Fall	4,595	3,783	275	5,104	4,947	1,304	181	6,484
Winter	404	2,150	3,390	1,269	519	1,452	2,416	3,138
Year 1943:								
Spring	1,894	8,562	372	790	3,295	8,791	469	1,647
Summer	3,991	4,937	960	4,019	3,769	4,160	1,618	8,232
Fall	3,170	4,083	231	2,548	4,909	2,769	415	7,292
Winter	94	372	1,078	406	160	655	2,082	1,814
Year 1944:								
Spring	732	2,678	278	290	3,262	8,807	1,762	2,479
Summer	2,255	1,289	669	1,272	8,215	3,018	5,616	11,093
Fall	2,285	1,963	39	535	9,811	5,373	172	9,292
Winter	85	423	340	115	509	1,717	5,271	4,347
Year 1945:								
Spring	122	743	52	123	3,778	7,029	776	3,060
Summer	322	1,185	623	853	3,210	2,296	4,511	10,302
Fall	1,801	1,660	990	990	6,934	2,369	1,387	8,570
Winter	7	250	1,469	484	148	866	5,024	6,337
Year 1946:								
Spring	15	681	26	287	2,871	6,707	1,749	1,722
Summer	2,497	1,876	548	2,294	9,238	4,118	2,922	11,547
Fall	2,506	1,546	110	4,985	9,897	3,690	372	14,644
Winter	412	1,560	217	1,560	851	5,302	1,329	5,807
Year 1947:								
Spring	1,105	3,906	288	338	4,884	11,914	1,280	1,615
Summer	2,793	1,242	959	3,343	4,644	2,111	3,147	9,288
Fall	9,935	1,357	63	9,518	7,279	1,148	71	9,170
Winter	1,648	1,866	242	2,902	656	836	461	5,856
Year 1948:								
Spring	2,594	1,692	210	1,680	5,764	3,113	218	3,715
Summer	5,523	1,064	1,432	4,650	3,519	678	1,868	6,733
Fall	9,925	1,998	32	4,027	5,786	1,245	14	7,102
Winter	4,232	3,824	350	1,323	2,874	1,649	488	4,201
Total, 1936–48:								
Spring	23,619	35,589	2,628	18,551	66,577	92,387	8,962	39,715
Summer	49,680	31,884	9,207	36,574	82,372	47,410	27,265	103,522
Fall	90,558	28,797	2,253	54,747	103,455	25,259	2,963	97,617
Winter	12,983	21,553	10,853	17,344	16,507	25,179	21,413	55,855

TABLE 2.—*Percentages of scrod, large, and total Georges Bank haddock landings by subareas and years, 1936 to 1948*

Year	Scrod					Large					Total				
	Northern Edge	Southeast Part	Southwest Part	South Channel	Total	Northern Edge	Southeast Part	Southwest Part	South Channel	Total	Northern Edge	Southeast Part	Southwest Part	South Channel	Total
1936	61.2	27.2	1.7	9.9	100	54.2	23.0	1.4	21.4	100	56.7	24.5	1.5	17.3	100
1937	68.5	12.2	.9	18.4	100	59.8	10.0	1.2	29.0	100	62.8	10.7	1.1	25.5	100
1938	56.0	16.1	.9	27.0	100	43.0	19.1	2.0	35.9	100	48.7	17.8	1.5	32.0	100
1939	36.5	21.5	2.2	39.8	100	33.9	24.0	2.6	39.5	100	35.0	22.9	2.4	39.7	100
1940	33.9	22.3	7.4	36.4	100	31.2	23.9	6.5	38.4	100	32.1	23.4	6.8	37.7	100
1941	24.0	33.8	8.6	33.6	100	21.0	36.4	7.8	34.8	100	22.3	35.2	8.2	34.3	100
1942	34.1	29.5	9.0	27.4	100	30.2	28.6	6.9	34.3	100	32.1	29.0	7.8	31.1	100
1943	24.4	47.9	7.0	20.7	100	23.3	31.4	8.8	36.5	100	23.8	38.3	8.1	29.8	100
1944	35.1	41.7	8.7	14.5	100	27.0	23.4	15.9	33.7	100	28.3	26.3	14.7	30.7	100
1945	19.3	32.9	26.8	21.0	100	21.1	18.8	17.6	42.5	100	20.8	21.0	18.9	39.3	100
1946	25.7	26.8	4.3	43.2	100	27.6	23.9	7.7	40.8	100	27.2	24.5	7.0	41.3	100
1947	36.4	20.5	3.8	39.3	100	27.1	24.9	7.7	40.3	100	30.7	23.2	6.2	39.9	100
1948	50.0	19.2	4.5	26.2	100	36.6	13.6	5.3	44.6	100	43.0	16.3	4.9	35.8	100
Weighted average	39.5	26.3	5.6	28.6	100	32.9	23.3	7.4	36.4	100	35.2	24.4	6.8	33.6	100
Unweighted average	38.8	27.0	6.6	27.5	100	33.5	23.2	7.0	36.3	100	35.6	24.1	6.8	33.5	100

TABLE 3.—*Scrod haddock landed, by seasons and years*
[In thousands of pounds]

Year	Spring	Summer	Fall	Winter	Total
1931	894	1,255	5,266	10,086	17,501
1932	6,955	8,737	11,799	4,022	31,513
1933	4,116	4,520	8,631	1,531	18,798
1934	1,605	3,488	6,038	1,845	12,976
1935	963	5,717	10,554	8,303	25,537
1936	3,872	9,604	12,933	3,541	29,950
1937	5,514	8,423	14,665	2,482	31,084
1938	4,307	7,982	20,414	7,204	39,907
1939	7,524	11,743	17,716	6,142	43,125
1940	6,614	9,393	9,507	4,086	29,600
1941	11,614	13,578	21,066	7,506	53,764
1942	11,484	17,026	13,757	7,213	49,480
1943	11,618	13,907	10,032	1,950	37,507
1944	3,978	5,485	4,822	963	15,248
1945	1,040	2,983	5,441	2,210	11,674
1946	1,009	7,215	9,147	3,749	21,120
1947	5,637	8,337	20,873	6,058	40,905
1948	6,176	12,669	15,982	9,729	44,556
Total	94,920	152,062	218,643	88,620	554,245
Average	5,273	8,448	12,147	4,923	30,791

TABLE 4.—*Large haddock landed, by seasons and years*
[In thousands of pounds]

Year	Spring	Summer	Fall	Winter	Total
1931	29,611	33,610	23,827	10,491	97,539
1932	18,136	19,534	23,303	12,934	73,907
1933	18,367	20,715	19,495	4,265	62,842
1934	7,261	13,953	12,780	2,914	36,908
1935	5,166	18,623	18,041	11,814	53,644
1936	13,828	17,218	16,359	6,663	54,068
1937	19,705	17,431	17,647	9,588	64,371
1938	15,283	15,637	12,834	8,726	52,480
1939	15,811	18,118	17,376	10,105	61,410
1940	15,763	22,204	16,490	8,588	63,045
1941	19,674	23,808	15,961	8,519	67,962
1942	16,870	20,300	12,916	7,525	57,611
1943	14,202	17,779	15,385	4,711	52,077
1944	16,310	27,942	24,648	11,844	80,744
1945	14,643	20,319	19,260	12,375	66,597
1946	13,049	27,825	28,603	13,289	82,766
1947	19,693	19,190	17,668	7,809	64,360
1948	12,810	12,798	14,147	9,212	48,967
Total	286,182	367,004	326,740	161,372	1,141,298
Average	15,899	20,389	18,152	8,965	63,405

TABLE 5.—*Total haddock landed, by seasons and years*
[In thousands of pounds]

Year	Spring	Summer	Fall	Winter	Total
1931	30,505	34,865	29,093	20,577	115,040
1932	25,091	28,271	35,102	16,956	105,420
1933	22,483	25,235	28,126	5,796	81,640
1934	8,866	17,441	18,818	4,759	49,884
1935	6,129	24,340	28,595	20,117	79,181
1936	17,700	26,822	29,292	10,204	84,018
1937	25,219	25,854	32,312	12,070	95,455
1938	19,590	23,619	33,248	15,930	92,387
1939	23,335	29,861	35,092	16,247	104,535
1940	22,377	31,597	25,997	12,674	92,645
1941	31,288	37,386	37,027	16,025	121,726
1942	28,354	37,326	26,673	14,738	107,091
1943	25,820	31,686	25,417	6,661	89,584
1944	20,288	33,427	29,470	12,807	95,992
1945	15,683	23,302	24,701	14,585	78,271
1946	14,058	35,040	37,750	17,038	103,886
1947	25,330	27,527	38,541	13,867	105,265
1948	18,986	25,467	30,129	18,941	93,523
Total	381,102	519,066	545,383	249,992	1,695,543
Average	21,172	28,837	30,299	13,888	94,196

AVERAGE WEIGHTS OF HADDOCK LANDED

Average weights of fish landed, in each season, year, subarea, and market category, were computed by combining length samples of haddock landed with seasonal length-weight relations. This procedure is described in the following paragraphs.

At the Boston Fish Pier, lengths of representative samples of the haddock landed were obtained from 1931 through 1948. In general, 50 scrod and 100 large haddock were measured from a "trip" when a vessel had fished in only one subarea of Georges Bank, and as many vessels were sampled as time permitted.

Each fish was measured from the tip of the snout to the fork of the tail. Lengths were recorded by centimeter groups, that is, fish measuring from 40.0 centimeters to and including 40.9 centimeters were recorded as 40 centimeters, fish from 41.0 centimeters to and including 41.9 centimeters as 41 centimeters, and so on. No distinction as to sex was possible as most haddock, when landed, are already dressed.

The numbers of Georges Bank haddock that were measured, by years, seasons, and market categories are shown in table 6. In all, measurements of 627,996 haddock from Georges Bank were utilized in this analysis.

Table 7 illustrates the general method used to compute the average weight of haddock landed. The steps of this method are as follows: (1) The number of fish of each centimeter size group in the total sample for the season was entered in column II; (2) the length-weight relation was available by seasons (table 8 and figure 7) and the average weights for each centimeter size group were listed in column III, the total weight of all fish measured of each centimeter size group was computed in column IV, and the total weight of *all sizes* in the season's sample was entered at the bottom of column IV; and finally (3) the total weight of the sample was divided by the number of fish in the sample to give the average weight of the fish in the sample. We used this same general method for each season, year, subarea, and market category.

Summaries of average weights are given in table 9 and figure 8; to save space, values for the various subareas are not shown.

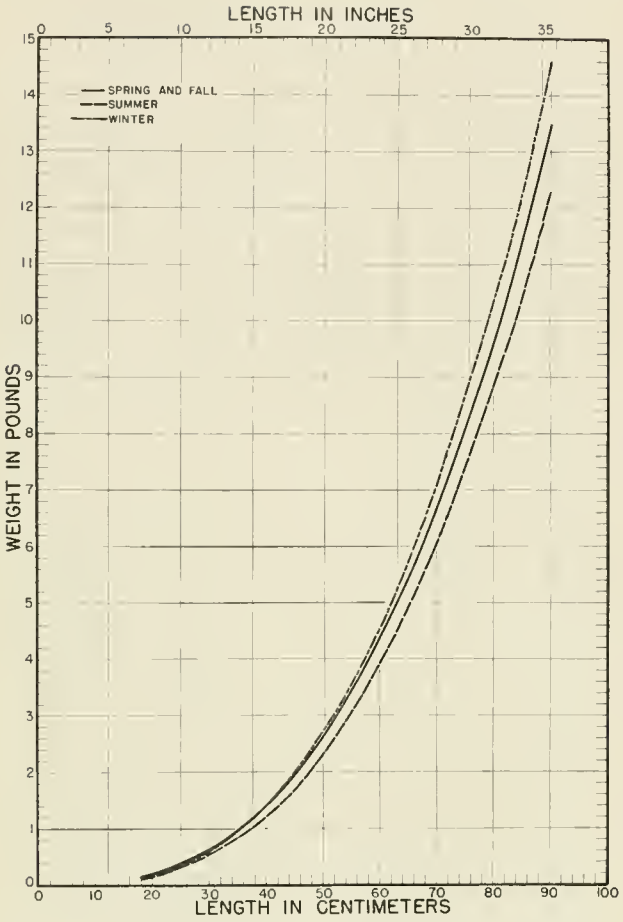


FIGURE 7.—Relation between length and weight for Georges Bank haddock, by seasons.

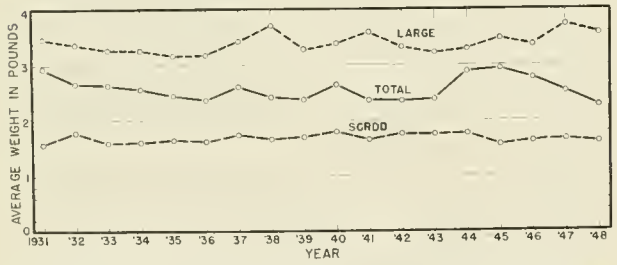


FIGURE 8.—Average weights of scrod, large, and total haddock landed from Georges Bank, by years.

TABLE 6.—*Numbers of haddock measured for length, by seasons and years*

Season	Scrod	Large	Total
Year 1931:			
Spring	513	5,042	5,555
Summer	1,194	4,054	5,248
Fall	3,285	4,577	7,862
Winter	4,102	2,562	6,664
Total	9,094	16,235	25,329
Year 1932:			
Spring	2,913	3,484	6,397
Summer	2,445	6,245	8,690
Fall	4,849	8,558	13,407
Winter	3,741	3,662	7,403
Total	13,948	21,949	35,897
Year 1933:			
Spring	3,082	3,834	6,914
Summer	1,702	3,775	5,477
Fall	2,455	5,349	7,804
Winter	911	2,157	3,068
Total	18,150	15,115	23,265
Year 1934:			
Spring	675	3,326	4,001
Summer	2,014	3,341	5,355
Fall	2,588	3,924	6,512
Winter	2,691	1,831	4,522
Total	7,968	12,422	20,390
Year 1935:			
Spring	1,440	3,398	4,838
Summer	4,582	7,357	11,939
Fall	7,199	6,462	13,661
Winter	3,318	2,981	6,299
Total	16,539	20,198	36,737
Year 1936:			
Spring	3,643	6,914	10,557
Summer	9,533	11,089	20,622
Fall	9,740	9,997	19,737
Winter	3,849	5,595	9,444
Total	26,765	33,595	60,360
Year 1937:			
Spring	3,383	8,781	12,164
Summer	5,394	8,777	14,171
Fall	5,129	5,296	10,425
Winter	4,055	5,387	9,442
Total	17,961	28,241	46,202
Year 1938:			
Spring	4,419	7,574	11,993
Summer	4,592	6,520	11,112
Fall	5,250	4,668	9,918
Winter	3,860	3,716	7,576
Total	18,121	22,478	40,599
Year 1939:			
Spring	2,540	4,002	6,542
Summer	5,244	6,835	12,079
Fall	4,448	7,712	12,160
Winter	3,043	4,141	7,184
Total	15,275	22,690	37,965

TABLE 6.—*Numbers of haddock measured for length, by seasons and years*—Continued

Season	Scrod	Large	Total
Year 1940:			
Spring	4,219	9,324	13,543
Summer	4,085	8,588	12,674
Fall	3,356	4,784	8,140
Winter	4,501	4,379	8,880
Total	16,162	27,075	43,237
Year 1941:			
Spring	6,080	8,145	14,225
Summer	5,287	6,069	11,356
Fall	8,167	6,179	14,346
Winter	4,853	3,334	8,187
Total	24,387	23,727	48,114
Year 1942:			
Spring	4,516	6,380	10,896
Summer	7,163	8,453	15,616
Fall	6,247	6,186	12,433
Winter	3,933	4,345	8,278
Total	21,859	25,364	47,223
Year 1943:			
Spring	6,082	6,644	12,726
Summer	4,796	4,834	9,630
Fall	3,237	6,420	9,657
Winter	644	2,304	2,948
Total	14,759	20,202	34,961
Year 1944:			
Spring	1,471	3,295	4,766
Summer	1,532	5,183	6,715
Fall	1,984	5,262	7,246
Winter	200	1,890	2,090
Total	5,187	15,630	20,817
Year 1945:			
Spring	250	1,644	1,894
Summer	649	1,797	2,446
Fall	950	3,150	4,100
Winter	699	3,266	3,965
Total	2,548	9,857	12,405
Year 1946:			
Spring	750	2,800	3,550
Summer	2,600	6,147	8,747
Fall	3,256	6,660	9,910
Winter	2,234	3,387	5,621
Total	8,834	18,994	27,828
Year 1947:			
Spring	2,230	3,651	5,881
Summer	2,037	2,870	4,907
Fall	3,776	7,861	11,637
Winter	3,205	4,468	7,673
Total	11,248	18,850	30,098
Year 1948:			
Spring	3,507	4,181*	7,688
Summer	3,480	2,217	5,697
Fall	7,101	7,417	14,518
Winter	4,763	3,903	8,666
Total	18,851	17,718	36,569
All years:			
Spring	51,713	92,419	144,132
Summer	68,330	104,151	172,481
Fall	83,011	110,462	193,473
Winter	54,602	63,308	117,910
Total	257,656	370,340	627,996

TABLE 7.—*Method used to compute average weight of haddock*

Example used: 1948, Spring, Southeast Part, Scrod

Length group [1] (I)	Number in sample (II)	Average weight (III)	Total weight of sample (IV)
		Pounds	*Pounds*
29 cm	1	0.58	0.58
30 cm	5	.64	3.20
31 cm	11	.70	7.70
32 cm	17	.76	12.92
33 cm	29	.83	24.07
34 cm	36	.90	32.40
35 cm	40	.98	39.20
36 cm	44	1.06	46.64
37 cm	45	1.14	51.30
38 cm	41	1.23	50.43
39 cm	31	1.32	40.92
40 cm	53	1.4	74.2
41 cm	54	1.5	81.0
42 cm	82	1.6	131.2
43 cm	133	1.7	226.1
44 cm	142	1.8	255.6
45 cm	188	2.0	376.0
46 cm	188	2.1	394.8
47 cm	183	2.2	402.6
48 cm	160	2.4	384.0
49 cm	160	2.5	400.0
50 cm	93	2.6	241.8
51 cm	62	2.8	173.6
52 cm	38	2.9	110.2
53 cm	17	3.1	52.7
54 cm	11	3.2	35.2
55 cm	6	3.4	20.4
56 cm	2	3.6	7.2
57 cm	----------	3.8	----------
58 cm	----------	4.0	----------
59 cm	1	4.2	4.2
Total	1,873	[2] 1,965	3,680.16

[1] By 1-cm. intervals.

[2] $\frac{3{,}680.16 \text{ pounds}}{1{,}873 \text{ fish}} = 1.965$ pounds.

TABLE 8.—*Length-weight relation by seasons, in terms of centimeter size groups and drawn weight in pounds*

Length [1]	Drawn weight in pounds			
	Spring	Summer	Fall	Winter
18 cm	0.15	0.12	0.15	0.14
19 cm	.17	.14	.17	.16
20 cm	.20	.17	.20	.19
21 cm	.23	.20	.23	.21
22 cm	.27	.23	.26	.25
23 cm	.30	.26	.30	.28
24 cm	.34	.29	.33	.32
25 cm	.38	.33	.38	.36
26 cm	.43	.36	.42	.40
27 cm	.47	.41	.47	.45
28 cm	.52	.45	.52	.50
29 cm	.58	.50	.57	.55
30 cm	.64	.55	.63	.61
31 cm	.70	.60	.69	.67
32 cm	.76	.66	.75	.73
33 cm	.83	.72	.82	.80
34 cm	.90	.79	.89	.88
35 cm	.98	.85	.96	.95
36 cm	1.06	.92	1.05	1.04
37 cm	1.14	1.00	1.13	1.12
38 cm	1.23	1.08	1.22	1.21
39 cm	1.32	1.16	1.31	1.31
40 cm	1.4	1.2	1.4	1.4
41 cm	1.5	1.3	1.5	1.5

See footnote at end of table.

TABLE 8.—*Length-weight relation by seasons, in terms of centimeter size groups and drawn weight in pounds*—Con.

Length [1]	Drawn weight in pounds			
	Spring	Summer	Fall	Winter
42 cm	1.6	1.4	1.6	1.6
43 cm	1.7	1.5	1.7	1.7
44 cm	1.8	1.6	1.8	1.8
45 cm	2.0	1.7	2.0	2.0
46 cm	2.1	1.8	2.1	2.1
47 cm	2.2	2.0	2.2	2.2
48 cm	2.4	2.1	2.3	2.4
49 cm	2.5	2.2	2.5	2.5
50 cm	2.6	2.3	2.6	2.7
51 cm	2.8	2.5	2.8	2.8
52 cm	2.9	2.6	2.9	3.0
53 cm	3.1	2.8	3.1	3.2
54 cm	3.2	2.9	3.2	3.4
55 cm	3.4	3.1	3.4	3.5
56 cm	3.6	3.2	3.6	3.7
57 cm	3.8	3.4	3.8	3.9
58 cm	4.0	3.6	4.0	4.1
59 cm	4.2	3.8	4.1	4.3
60 cm	4.4	3.9	4.3	4.5
61 cm	4.6	4.1	4.5	4.8
62 cm	4.8	4.3	4.8	5.0
63 cm	5.0	4.5	5.0	5.2
64 cm	5.2	4.7	5.2	5.5
65 cm	5.4	4.9	5.4	5.7
66 cm	5.7	5.1	5.6	6.0
67 cm	5.9	5.4	5.9	6.2
68 cm	6.2	5.6	6.1	6.5
69 cm	6.4	5.8	6.4	6.8
70 cm	6.7	6.1	6.7	7.1
71 cm	7.0	6.3	6.9	7.4
72 cm	7.2	6.6	7.2	7.7
73 cm	7.5	6.8	7.5	8.0
74 cm	7.8	7.1	7.8	8.3
75 cm	8.1	7.4	8.1	8.7
76 cm	8.4	7.7	8.4	9.0
77 cm	8.7	7.9	8.7	9.4
78 cm	9.0	8.2	9.0	9.7
79 cm	9.3	8.6	9.3	10.1
80 cm	9.7	8.9	9.6	10.4
81 cm	10.0	9.2	10.0	10.8
82 cm	10.3	9.5	10.3	11.1
83 cm	10.6	9.8	10.6	11.5
84 cm	10.9	10.1	10.9	11.8
85 cm	11.4	10.3	11.4	12.3
86 cm	11.7	10.7	11.7	12.7
87 cm	12.2	11.2	12.2	13.1
88 cm	12.6	11.5	12.6	13.6
89 cm	12.9	11.8	12.9	14.1
90 cm	13.5	12.3	13.5	14.6

See footnote at end of table.

[1] Size groups by 1-cm. intervals.

TABLE 9.—*Average weights in pounds of scrod, large, and total haddock, by seasons and years*

Year	Scrod					Large					Total				
	Spring	Summer	Fall	Winter	Total	Spring	Summer	Fall	Winter	Total	Spring	Summer	Fall	Winter	Total
1931	1.817	1.540	1.653	1.541	1.585	3.648	3.112	3.866	3.490	3.473	3.543	3.079	3.112	2.154	2.940
1932	1.654	1.679	1.942	1.921	1.793	3.732	3.350	3.184	3.322	3.374	2.769	2.562	2.621	2.832	2.670
1933	1.938	1.248	1.714	1.636	1.604	3.607	3.062	3.171	3.639	3.277	3.116	2.429	2.515	2.750	2.643
1934	1.890	1.648	1.614	1.402	1.617	3.580	3.126	3.271	3.195	3.263	3.082	2.650	2.460	2.136	2.580
1935	1.874	1.594	1.705	1.624	1.658	3.706	3.014	3.044	3.476	3.174	3.212	2.492	2.360	2.363	2.451
1936	1.905	1.456	1.710	1.586	1.626	3.602	3.009	3.025	3.343	3.187	3.014	2.177	2.267	2.415	2.374
1937	1.950	1.528	1.820	1.793	1.748	3.580	3.160	3.289	4.051	3.432	3.027	2.344	2.407	3.218	2.613
1938	1.972	1.510	1.709	1.656	1.679	4.902	3.199	3.348	3.819	3.716	3.692	2.322	2.107	2.401	2.438
1939	1.890	1.633	1.718	1.674	1.715	3.955	3.083	2.933	3.492	3.285	2.925	2.285	2.161	2.475	2.384
1940	1.989	1.748	1.867	1.558	1.803	3.434	3.218	3.357	3.998	3.399	2.827	2.575	2.598	2.656	2.650
1941	1.688	1.541	1.681	1.823	1.662	3.991	3.330	3.377	4.030	3.592	2.650	2.342	2.145	2.572	2.375
1942	2.012	1.690	1.701	1.742	1.766	3.644	3.195	3.121	3.536	3.340	2.743	2.272	2.182	2.351	2.366
1943	1.924	1.586	1.837	1.809	1.757	3.495	3.138	3.306	2.774	3.239	2.555	2.195	2.513	2.400	2.393
1944	1.926	1.617	1.800	2.049	1.772	3.464	3.031	3.231	3.965	3.290	2.995	2.651	2.859	3.705	2.896
1945	1.940	1.296	1.644	1.736	1.573	3.678	3.157	3.548	3.766	3.481	3.472	2.667	2.827	3.199	2.948
1946	1.665	1.449	1.770	1.778	1.642	3.630	3.077	3.406	3.824	3.377	3.346	2.499	2.782	3.052	2.780
1947	1.876	1.481	1.580	2.291	1.670	3.725	3.635	3.622	4.194	3.719	3.055	2.524	2.130	3.077	2.519
1948	1.842	1.493	1.681	1.592	1.623	3.959	3.251	3.472	3.743	3.572	2.882	2.050	2.218	2.209	2.272
Weighted average	1.871	1.556	1.719	1.697	1.691	3.718	3.163	3.306	3.661	3.398	2.984	2.430	2.413	2.596	2.554

NUMBERS OF HADDOCK LANDED

Dividing poundage by average weight gave the number of fish landed—for each season, subarea, market category, and year. Excepting subarea values, all of these numbers are shown in the following tables.

Tables 10, 11, and 12 show the numbers of scrod, large, and total haddock landed, by seasons and years. Relative contributions of scrod and large haddock to the total, by seasons, are shown in figure 9. Figure 10 shows the yearly trends, and here it can be seen that much of the variation in total landings by years is due to variations in scrod landings. The importance of these small-sized haddock to the present fishery is thus evident.

SIZE COMPOSITIONS OF HADDOCK LANDED

Now having available the number of haddock that were landed (in each season, year, subarea, and market category), and having also the lengths of samples of haddock (in each similar subdivision), we estimated how many haddock of each size were landed. This was accomplished by multiplying the number of fish measured in each centimeter size group by the proportion of the number landed to the number measured. This

calculation assumes that the fish measured were representative samples of the landings. Precautions had been taken to avoid bias in sampling, and many uniformity trials showed that the samples could be considered as representative of the landing.

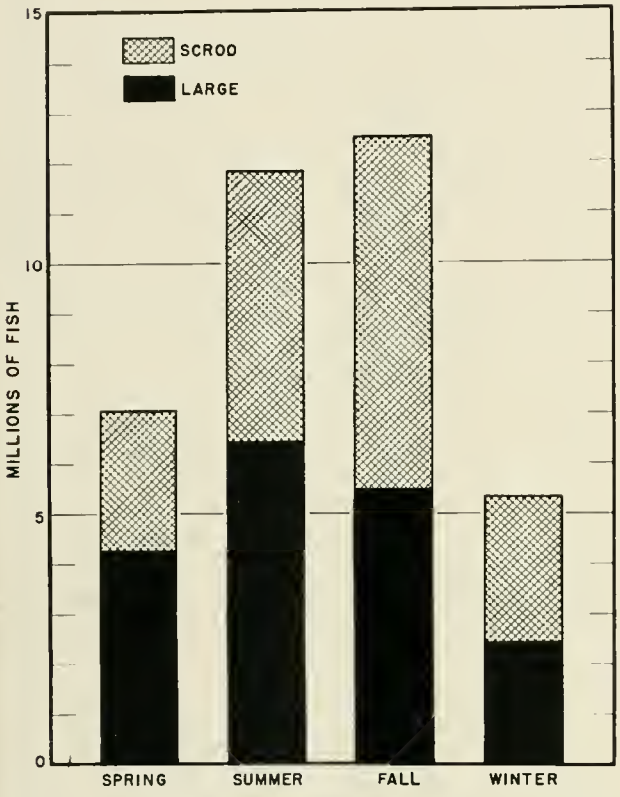


FIGURE 9.—Numbers of scrod, large, and total haddock landed from Georges Bank in the average year, by seasons.

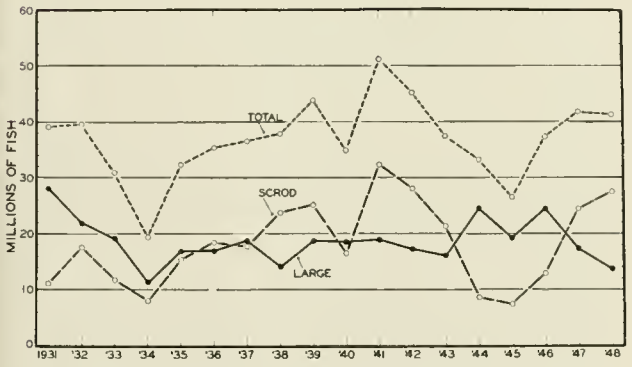


FIGURE 10.—Numbers of scrod, large, and total haddock landed from Georges Bank, by years.

TABLE 10.—*Numbers of scrod haddock landed, by seasons and years*

[In thousands of fish]

Year	Spring	Summer	Fall	Winter	Total
1931	492	816	3,186	6,547	11,041
1932	4,204	5,206	6,075	2,094	17,579
1933	2,124	3,623	5,035	936	11,718
1934	849	2,117	3,742	1,316	8,024
1935	514	3,587	6,190	5,113	15,404
1936	2,033	6,598	7,561	2,232	18,424
1937	2,828	5,512	8,056	1,384	17,780
1938	2,193	5,285	11,945	4,350	23,773
1939	3,980	7,190	10,313	3,670	25,153
1940	3,325	5,373	5,093	2,623	16,414
1941	6,879	8,811	12,535	4,117	32,342
1942	5,708	10,077	8,088	4,140	28,013
1943	6,040	8,771	5,460	1,078	21,349
1944	2,065	3,393	2,679	470	8,607
1945	536	2,301	3,310	1,273	7,420
1946	606	4,978	5,169	2,108	12,861
1947	3,004	5,628	13,213	2,644	24,489
1948	3,352	8,484	9,510	6,113	27,459
Total	50,732	97,750	127,160	52,208	327,850
Average	2,818	5,431	7,065	2,900	18,214

TABLE 11.—*Numbers of large haddock landed, by seasons and years*

[In thousands of fish]

Year	Spring	Summer	Fall	Winter	Total
1931	8,117	10,799	6,164	3,006	28,086
1932	4,859	5,831	7,318	3,894	21,902
1933	5,092	6,765	6,147	1,172	19,176
1934	2,028	4,464	3,907	912	11,311
1935	1,394	6,179	5,927	3,399	16,899
1936	3,839	5,723	5,408	1,993	16,963
1937	5,504	5,517	5,366	2,367	18,754
1938	3,118	4,888	3,833	2,285	14,124
1939	3,998	5,876	5,924	2,894	18,692
1940	4,590	6,899	4,912	2,148	18,549
1941	4,930	7,150	4,726	2,114	18,920
1942	4,630	6,353	4,138	2,128	17,249
1943	4,064	5,665	4,653	1,698	16,080
1944	4,708	9,218	7,629	2,987	24,542
1945	3,981	6,436	5,428	3,287	19,132
1946	3,595	9,043	8,399	3,475	24,512
1947	6,287	5,279	4,878	1,862	17,306
1948	3,236	3,937	4,075	2,461	13,709
Total	76,970	116,022	98,832	44,082	335,906
Average	4,276	6,445	5,491	2,449	18,661

TABLE 12.—*Numbers of total haddock landed, by seasons and years*

[In thousands of fish]

Year	Spring	Summer	Fall	Winter	Total
1931	8,609	11,615	9,350	9,553	39,127
1932	9,063	11,037	13,393	5,988	39,481
1933	7,216	10,388	11,182	2,108	30,894
1934	2,877	6,581	7,649	2,228	19,335
1935	1,908	9,766	12,117	8,512	32,303
1936	5,872	12,321	12,969	4,225	35,387
1937	8,332	11,029	13,422	3,751	36,534
1938	5,311	10,173	15,778	6,635	37,897
1939	7,978	13,066	16,237	6,564	43,845
1940	7,915	12,272	10,005	4,771	34,963
1941	11,809	15,961	17,261	6,231	51,262
1942	10,338	16,430	12,226	6,268	45,262
1943	10,104	14,436	10,113	2,776	37,429
1944	6,773	12,611	10,308	3,457	33,149
1945	4,517	8,737	8,738	4,560	26,552
1946	4,201	14,021	13,568	5,583	37,373
1947	8,291	10,907	18,091	4,506	41,795
1948	6,588	12,421	13,585	8,574	41,168
Total	127,702	213,772	225,992	96,290	663,756
Average	7,095	11,876	12,555	5,349	36,875

The size compositions for subareas were combined, and thus we obtained a size composition representing all of Georges Bank, for each season, year, and market category. A certain amount of irregularity in these curves was due to sampling variations, inasmuch as only a limited sample from a very large population of fish had been obtained. To eliminate some of this irregularity we smoothed each distribution by a moving average of three.

Scrod haddock

Tables 13, 14, 15, and 16 show the size compositions [3] of the landings of scrod, in each of the 72 seasons, from 1931 through 1948. Table 17 shows the size compositions of scrod by years. Table 18 and figure 11 show the average size compositions of scrod for each season in all of the 18 years, and table 19 shows the size composition of scrod that were landed in the average year, and also the percentage size composition.

Large haddock

Tables 20, 21, 22, and 23 show the size compositions of large haddock in each of the 72 seasons over the 18-year period. Table 24 shows the size composition of large haddock by years. Table 25 and figure 11 show, by seasons, the average size composition of large haddock that were landed in all 18 years, and table 26 shows the size composition of large haddock that were landed in the average year, and also the percentage size composition.

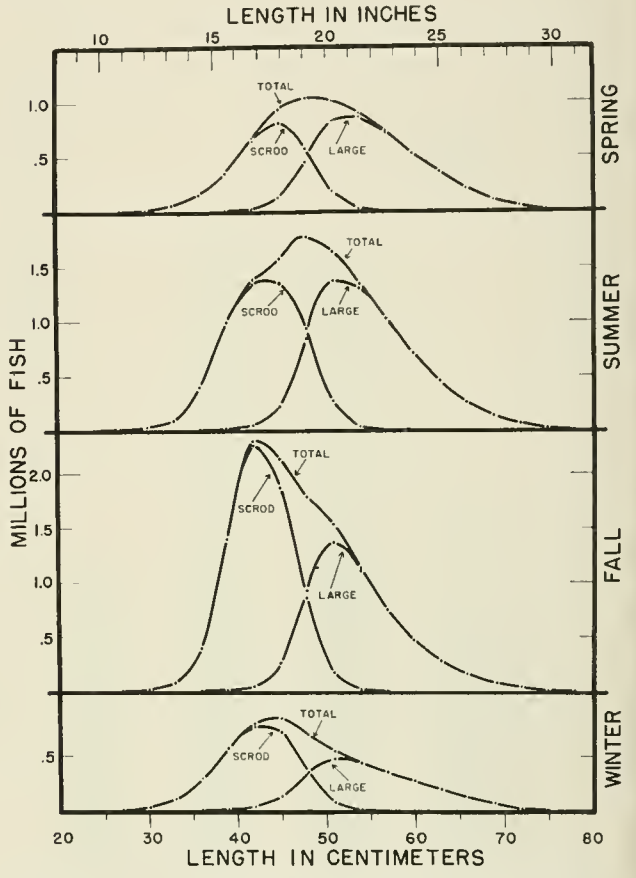


FIGURE 11.—Size compositions of scrod, large, and total haddock landed from Georges Bank in the average year, by seasons.

Total haddock

Tables 27, 28, 29, and 30, and figures 12a, 12b, and 12c show the size compositions of total haddock (scrod and large combined) in each of the 72 seasons over the 18-year period.

The presence of modes (figures 12a, 12b, and 12c), at slightly increasing sizes of fish in succeeding seasons, suggests that each series of modes may be composed largely of the same year class of haddock. In some instances these year classes (if they are year classes) apparently were the chief source of supply of the fishery for several succeeding seasons, and even for succeeding years.

These modes are more obvious if one season (spring, for example) in a particular year is com-

[3] For convenience in handling the large mass of data, we grouped all length frequencies by 3-centimenter groups: Fish of the 29-, 30-, and 31-centimeter groups were recorded as 30 centimeters, fish of the 32-, 33-, and 34-centimeter groups as 33 centimeters, and so on. In graphs and tables where centimeters are shown, they are shown as 30, 33, and 36 rather than 30.5, 33.5, and 36.5 (the true midpoints of the groups) inasmuch as the original centimeter measurements were recorded as 29 when the midpoint was 29.5, 30 instead of 30.5, 31 instead of 31.5, etc. Where inches are shown in graphs, they represent actual values: The inch equivalents opposite 30.5 rather than 30, opposite 31.5 rather than 31, and so on.

The sizes in inches corresponding to the true midpoints of the 3-centimeter groups are as follows:

3-centimeter groups:	*Inches*
18 cm	7.3
21 cm	8.5
24 cm	9.6
27 cm	10.8
30 cm	12.0
33 cm	13.2
36 cm	14.4
39 cm	15.6
42 cm	16.7
45 cm	17.9
48 cm	19.1
51 cm	20.3
54 cm	21.6
57 cm	22.6
60 cm	23.8
63 cm	25.0
66 cm	26.2
69 cm	27.4
72 cm	28.5
75 cm	29.7
78 cm	30.9
81 cm	32.1
84 cm	33.3
87 cm	34.4

pared with the average of that season for all years. Figures 13a, 13b, and 13c show such contrasts in terms of deviations from seasonal means.

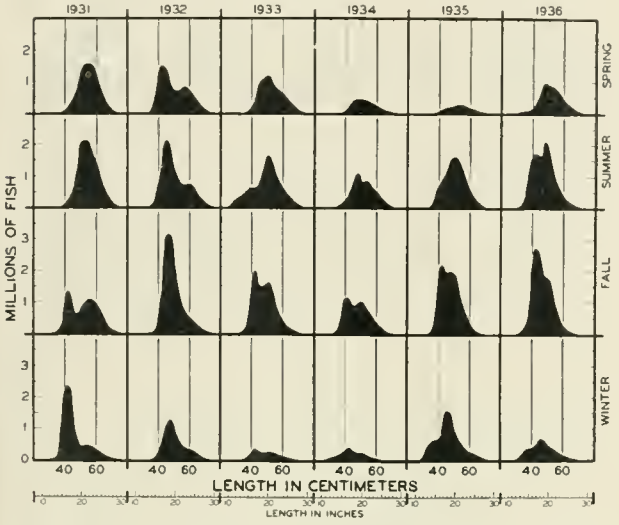


FIGURE 12a.—Size compositions of total haddock landings from Georges Bank, by seasons and years, 1931 to 1936.

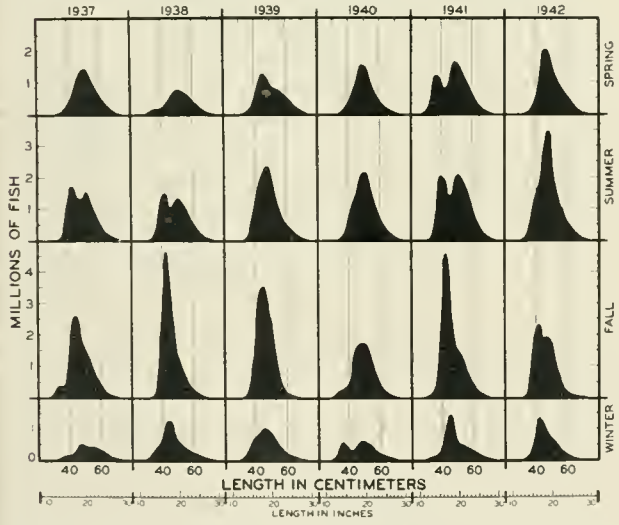


FIGURE 12b.—Size compositions of total haddock landings from Georges Bank, by seasons and years, 1937 to 1942.

Table 31 and figure 14 show the yearly size compositions for total haddock. Table 32 shows the four seasonal size compositions for the average of all 18 years. These values are shown also in figure 11.

In figure 14, it can be seen that there was considerable variation in the relative numbers of various sizes in different years. To study these differences more readily, we plotted (fig. 15) devia-

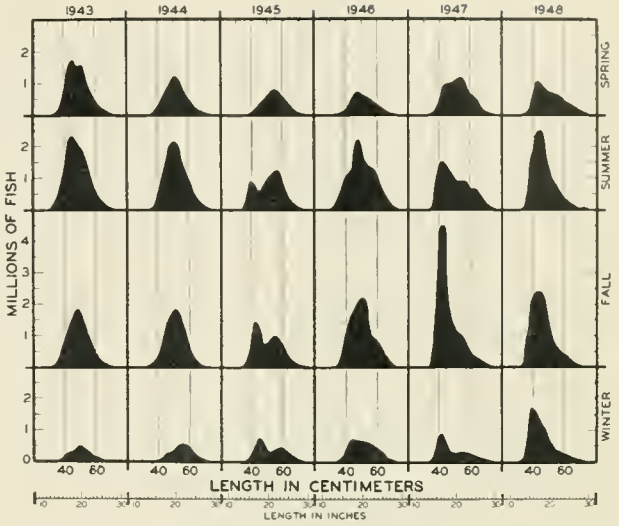


FIGURE 12c.—Size compositions of total haddock landings from Georges Bank, by seasons and years, 1943 to 1948.

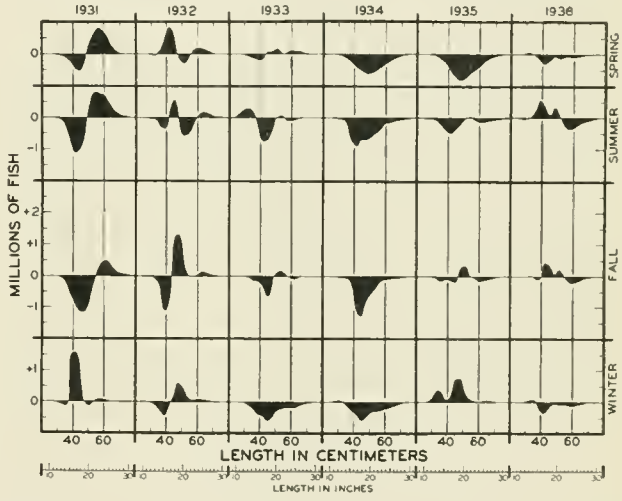


FIGURE 13a.—Deviations from the average size compositions, by seasons, 1931 to 1936.

tions from the average year. Here, it can be seen that a scarcity of small-sized fish characterized some years such as 1931, 1940, 1944, 1945, and 1946. In other years, such as 1943 and 1948, a scarcity of large-sized fish occurred. In still others, an abundance of either small-sized or large-sized haddock occurred, or a scarcity or an abundance of both—the scarce years of 1933, 1934, and 1935, and the abundant year of 1941 demonstrate this. In other years, such as 1937, all sizes were taken in approximately average numbers.

The differences in size composition help to explain how different average weights (shown in table 9) occurred. As one example, the years 1936

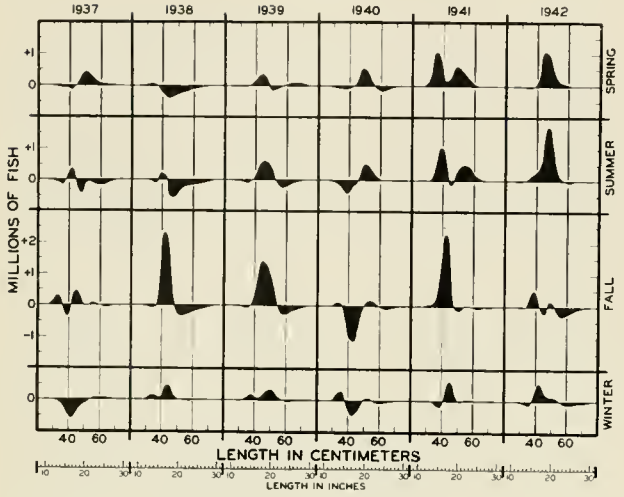


FIGURE 13b.—Deviations from the average size compositions, by seasons, 1937 to 1942.

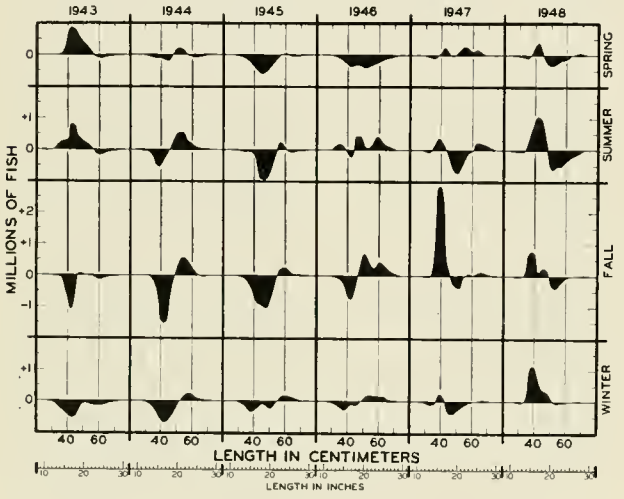


FIGURE 13c.—Deviations from the average size compositions, by seasons, 1943 to 1948.

and 1941 had an identical, low average weight of 2.37 pounds. In 1936, this low average weight was associated with a slight abundance of small-sized and a scarcity of large-sized haddock, while in 1941 it was associated with factors entirely different—an abundance of all sizes, but with small haddock much more abundant than large-sized haddock.

It is obvious that average weight is dependent upon the relative numbers of the various sizes and not upon the actual numbers of fish of various sizes.

In table 33 are shown the size composition of the average year and the percent size composition.

Undersized haddock

The New England Fish Exchange defines scrod haddock as 1½ to 2½ pounds. The average length

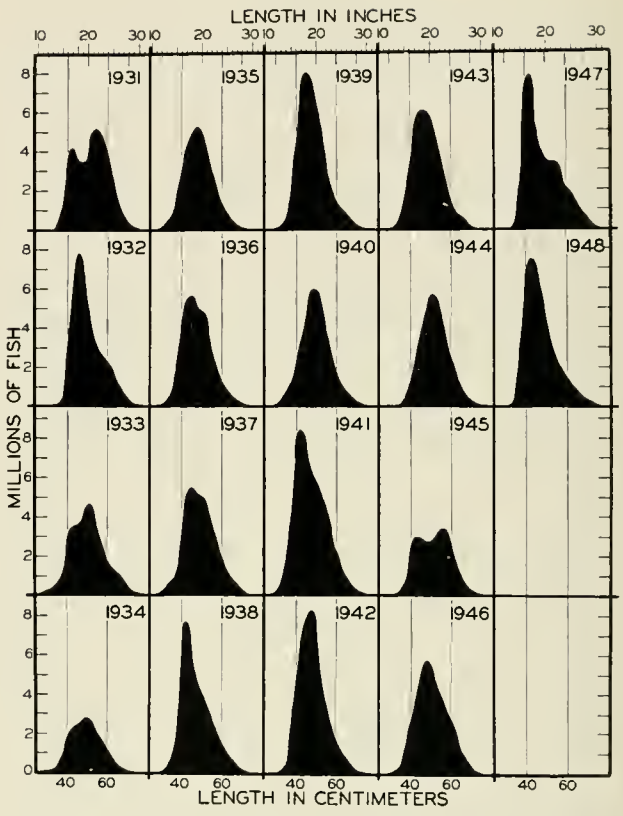


FIGURE 14.—Size compositions of total haddock landings from Georges Bank, by years.

of 1½ pound haddock is about 41 centimeters. Thus, most fish up to and including the 39-centimeter size group could be considered as undersized. From table 33, we see that in the average year about 4,974,000 undersized fish were landed, or 13.5 percent of the total. In all years the total number of undersized haddock landed was about 89,513,000. The numbers of undersized haddock that were landed in each year are shown in table 34.

Scrod versus large haddock

Table 35 shows the percentages of each size group that were scrod and large haddock; figure 16 shows the actual size compositions of scrod and large haddock.

The dividing line between scrod and large haddock for the average of the 18-year period was about 48 centimeters. Below 48 centimeters most fish landed were classified as scrod; above 48 most were classified as large haddock.

This dividing line has varied from year to year, owing to differences in relative abundance of fish of difference sizes and to market conditions. Such

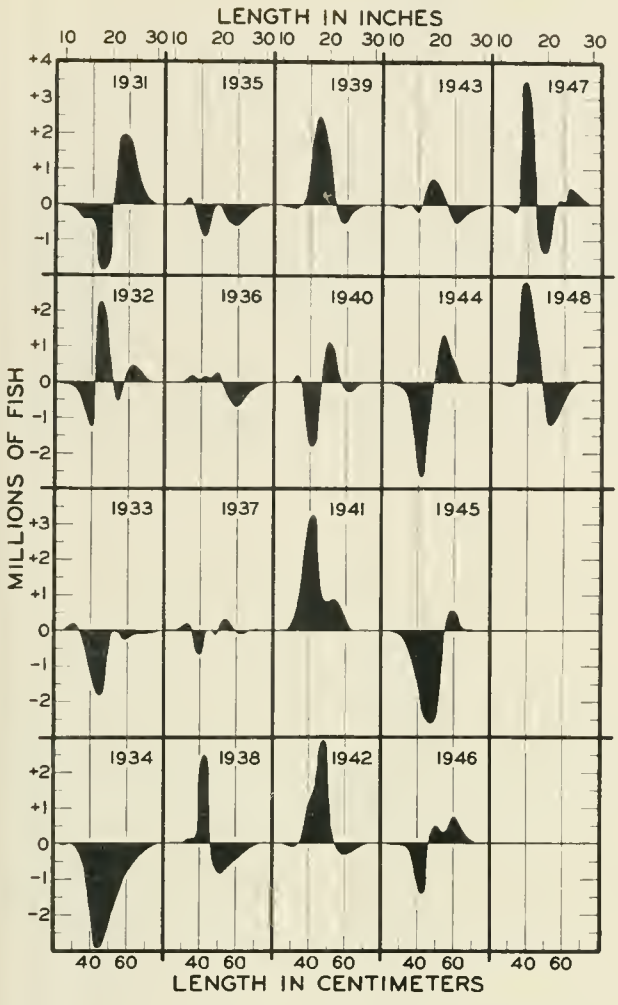
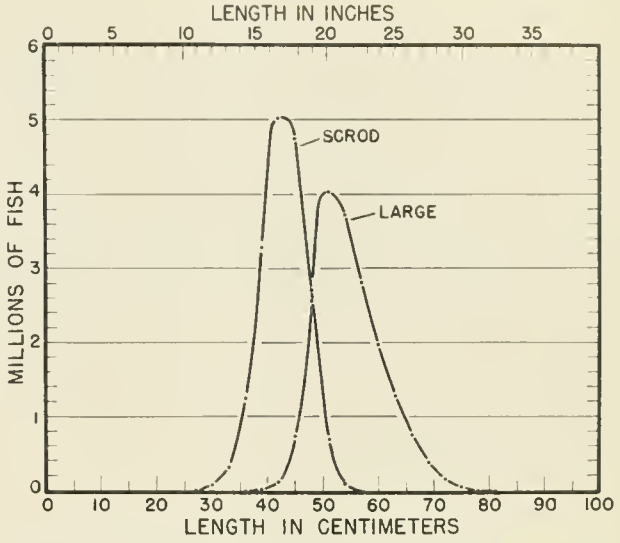


FIGURE 15.—Deviations from average size compositions, by years.



FIGURES 16.—Size compositions of scrod and large haddock landings from Georges Bank in average year.

variation made it necessary to measure samples of each category in every year for which we desired an accurate measurement of size composition of the total haddock landings.

The amount of overlap in length between the two market categories has been considerable. For instance, haddock as long as 63 centimeters were occasionally landed as scrod, and fish as small as 36 centimeters were landed as large haddock. This was due to difficulties and mistakes in sorting haddock into two arbitrary categories at sea under varying conditions of weather, haste, and so on.

TABLE 13.—*Size compositions of scrod haddock, spring seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
21 cm.							1				1							
24 cm.							1				3							
27 cm.						1		2			13		1					
30 cm.	1	7				28	9	30	9		108	5	12	2		8		
33 cm.	1	31	2	2	1	74	40	113	37	16	555	33	63	11		15	10	2
36 cm.	15	292	44	14	13	98	105	173	162	101	1,211	125	208	62	2	38	75	87
39 cm.	56	927	172	62	68	152	278	185	460	295	1,121	385	774	250	30	97	382	531
42 cm.	160	1,464	491	242	144	370	554	314	962	654	819	1,117	1,536	480	144	198	892	1,036
45 cm.	175	1,111	828	348	163	650	866	520	1,231	989	1,184	1,948	1,667	614	230	188	899	925
48 cm.	68	331	478	156	94	520	726	542	851	911	1,249	1,530	1,155	481	112	57	549	574
51 cm.	14	39	102	24	28	117	215	253	234	311	533	493	441	145	13	5	171	173
54 cm.	2	2	7	1	3	17	29	45	31	43	78	71	116	17	3		26	24
57 cm.						6	4	11	2	5	4	1	36	3	2			
60 cm.								4	1				18					
63 cm.								1					8					
66 cm.													3					
69 cm.													1					
72 cm.													1					
Total	492	4,204	2,124	849	514	2,033	2,828	2,193	3,980	3,325	6,879	5,708	6,040	2,065	536	606	3,004	3,352

[1] Size groups by 3-cm. intervals.

TABLE 14.—*Size compositions of scrod haddock, summer seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
21 cm						1												
24 cm			14			2		1			2							
27 cm			152			5		3			4	1	1			11		
30 cm		1	290	2	1	19		16	1		15	10	24	4		29		
33 cm		16	373	12	13	128	17	62	25	9	163	106	214	10	29	210	17	52
36 cm	8	114	524	103	189	635	265	396	345	134	949	531	655	85	333	555	556	696
39 cm	74	659	636	225	623	1,550	1,119	1,275	1,059	587	2,046	1,230	1,276	442	868	940	1,366	1,758
42 cm	240	1,594	592	472	899	1,702	1,722	1,477	1,768	1,176	1,925	1,758	2,166	996	688	1,033	1,515	2,420
45 cm	324	1,807	593	750	1,028	1,365	1,343	980	2,048	1,427	1,402	2,724	2,254	1,100	261	1,372	1,249	2,341
48 cm	152	842	347	463	656	900	718	769	1,502	1,416	1,491	2,706	1,575	636	104	714	732	1,068
51 cm	17	159	92	83	154	258	218	267	405	564	693	885	539	112	17	104	177	135
54 cm	1	14	9	5	20	29	54	33	31	56	107	116	57	8	1	8	16	12
57 cm			1	1	4	3	36	5	6	4	14	10	8					
60 cm				1		1	18	1					2			1		2
63 cm							2									1		
Total	816	5,206	3,623	2,117	3,587	6,598	5,512	5,285	7,190	5,373	8,811	10,077	8,771	3,393	2,301	4,978	5,628	8,484

[1] Size groups by 3-cm. intervals.

TABLE 15.—*Size compositions of scrod haddock, fall seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
24 cm							2				1							
27 cm			1			4	30			6	10	1			1	1		
30 cm	1		17	2	1	17	166	1	1	48	59	5	3	3	6	8	4	4
33 cm	7	1	44	41	24	103	383	40	43	183	136	58	41	50	12	36	54	104
36 cm	127	29	254	362	256	345	385	370	354	242	664	648	337	139	174	267	1,122	1,076
39 cm	736	318	1,228	1,094	1,310	1,298	1,050	2,291	1,591	414	2,519	1,901	836	315	812	884	4,250	2,158
42 cm	1,299	1,547	1,943	1,096	2,173	2,690	2,444	4,587	3,262	1,191	4,546	2,294	1,221	732	1,244	1,496	4,482	2,389
45 cm	777	2,592	1,121	693	1,648	2,172	2,395	3,359	3,178	1,535	3,180	1,785	1,553	929	798	1,504	2,205	2,262
48 cm	203	1,362	373	385	660	776	994	1,092	1,546	1,076	1,106	1,095	1,162	418	213	798	921	1,241
51 cm	28	203	53	67	111	140	188	177	308	347	277	264	281	77	32	164	147	236
54 cm	7	21	1	1	7	14	19	25	27	47	35	34	24	14	16	11	24	32
57 cm	1	2		1		2		3	3	3	2	3	2	2	2		4	6
60 cm										1								2
Total	3,186	6,075	5,035	3,742	6,190	7,561	8,056	11,945	10,313	5,093	12,535	8,088	5,460	2,679	3,310	5,169	13,213	9,510

[1] Size groups by 3-cm. intervals

TABLE 16.—*Size compositions of scrod haddock, winter seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
24 cm					2													
27 cm				16	11	5	2	4	2	1	7	1						
30 cm	1			80	140	37	18	67	28	63	55	10				3		4
33 cm	34	1	14	109	485	168	74	243	135	321	114	49	5	5	7	24	32	105
36 cm	694	19	68	176	632	343	149	418	434	566	169	204	63	28	37	107	254	893
39 cm	2,054	152	189	292	643	362	155	644	719	419	403	779	199	52	192	330	813	1,712
42 cm	2,264	567	362	389	989	460	210	1,199	826	288	1,076	1,351	274	79	448	661	878	1,537
45 cm	1,205	845	231	204	1,345	565	395	1,176	887	450	1,412	1,076	281	191	457	595	444	1,132
48 cm	274	445	63	44	718	250	292	481	510	384	698	523	208	107	120	296	177	576
51 cm	19	59	8	6	136	36	79	105	116	113	156	132	40	8	11	74	42	134
54 cm	1	6	1		11	5	9	11	12	17	26	14	7		1	14	3	17
57 cm	1				1	1	1	2	1	1	1	1	1			3	1	3
60 cm																1		
Total	6,547	2,094	936	1,316	5,113	2,232	1,384	4,350	3,670	2,623	4,117	4,140	1,078	470	1,273	2,108	2,644	6,113

[1] Size groups by 3-cm. intervals.

TABLE 17.—*Size composition, scrod haddock, in each of the 18 years*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
21 cm						1	1				1							
24 cm			14		2	2	3	1			6							
27 cm			153	16	11	15	32	9	2	7	34	3	2		1	12		
30 cm	3	8	307	84	142	101	193	114	39	111	237	30	39	9	6	48	4	8
33 cm	42	49	433	164	523	473	514	458	240	529	968	246	323	76	48	285	113	263
36 cm	844	454	890	655	1,090	1,421	904	1,357	1,295	1,043	2,993	1,508	1,263	314	546	967	2,007	2,752
39 cm	2,920	2,056	2,225	1,673	2,644	3,362	2,602	4,395	3,829	1,715	6,089	4,295	3,085	1,059	1,902	2,251	6,811	6,159
42 cm	3,963	5,172	3,388	2,199	4,205	5,222	4,930	7,577	6,818	3,309	8,366	6,520	5,197	2,287	2,524	3,388	7,767	7,382
45 cm	2,481	6,355	2,773	1,995	4,184	4,752	4,999	6,035	7,344	4,401	7,178	7,533	5,755	2,834	1,746	3,659	4,797	6,660
48 cm	697	2,980	1,261	1,048	2,128	2,446	2,730	2,884	4,409	3,787	4,544	5,854	4,100	1,642	549	1,865	2,379	3,459
51 cm	78	460	255	180	429	551	700	802	1,063	1,335	1,659	1,774	1,301	342	73	347	537	678
54 cm	11	43	18	7	41	65	111	114	101	163	246	235	204	39	21	33	69	85
57 cm	2	2	1	2	5	12	41	21	12	13	21	15	47	5	4	3	5	9
60 cm				1		1	18	5	1	1			20			2		4
63 cm							2	1					8			1		
66 cm													3					
69 cm													1					
72 cm													1					
Total	11,041	17,579	11,718	8,024	15,404	18,424	17,786	23,773	25,153	16,414	32,342	28,013	21,349	8,607	7,420	12,861	24,489	27,459

[1] Size groups by 3-cm. intervals.

TABLE 18.—*Average size composition of scrod haddock, in each of the seasons*

[In thousands of fish]

Length [1]	Spring	Summer	Fall	Winter
24 cm		1		
27 cm	1	10	3	3
30 cm	12	23	19	28
33 cm	56	81	76	107
36 cm	157	393	397	292
39 cm	346	985	1,389	562
42 cm	643	1,341	2,258	770
45 cm	808	1,354	1,871	716
48 cm	577	933	857	342
51 cm	184	271	172	71
54 cm	29	32	20	9
57 cm	4	5	2	1
60 cm	1	1		
63 cm	1			
Total	2,819	5,430	7,064	2,901

[1] Size groups by 3-cm. intervals.

TABLE 19.—*Size composition of scrod haddock in the average year*

[In thousands of fish]

Length [1]	Average number	Percent of total
24 cm	1	
27 cm	17	0.1
30 cm	82	.4
33 cm	320	1.8
36 cm	1,240	6.8
39 cm	3,281	18.0
42 cm	5,012	27.5
45 cm	4,747	26.1
48 cm	2,710	14.9
51 cm	699	3.8
54 cm	89	.5
57 cm	12	.1
60 cm	3	
63 cm	1	
Total	18,214	100.0

[1] Size groups by 3-cm. intervals.

TABLE 20.—*Size compositions of large haddock, spring seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
30 cm																1		
33 cm																		
36 cm								1						1		4	1	
39 cm	6	1		1		1	2	4	2	1		1	4	7	3	20	3	
42 cm	36	40	16	5	4	9	8	7	7	9	3	10	15	36	25	118	16	11
45 cm	256	279	181	67	44	89	118	38	36	112	51	75	73	148	112	444	96	45
48 cm	825	548	637	276	132	450	636	192	282	647	395	462	416	596	395	663	461	206
51 cm	1,398	684	1,074	410	240	777	1,225	526	652	1,171	1,025	945	958	1,068	673	608	946	526
54 cm	1,567	753	897	394	289	798	1,171	658	778	1,018	1,169	992	978	1,045	791	551	1,139	627
57 cm	1,537	834	753	317	233	668	897	599	715	683	940	824	686	732	728	453	971	590
60 cm	1,185	714	632	231	178	435	608	444	560	402	604	586	416	477	585	322	641	410
63 cm	742	497	450	153	140	306	412	306	416	241	363	382	252	283	350	228	545	346
66 cm	364	300	282	99	76	174	232	183	266	160	198	197	162	172	185	109	275	228
69 cm	132	148	118	47	38	87	122	92	167	88	101	94	67	84	87	46	122	162
72 cm	51	43	41	18	17	34	54	44	78	42	52	44	25	39	32	19	63	64
75 cm	18	16	7	6	3	10	17	19	26	10	23	14	8	16	15	9	7	19
78 cm		2	4	4		1	2	5	10	5	5	4	4	4			1	1
81 cm									2	1	1							1
84 cm									1									
Total	8,117	4,859	5,092	2,028	1,394	3,839	5,504	3,118	3,998	4,590	4,930	4,630	4,064	4,708	3,981	3,595	5,287	3,236

[1] Size groups by 3-cm. intervals.

TABLE 21.—*Size compositions of large haddock, summer seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
33 cm																1		
36 cm						1		1						1	11	15		
39 cm	1	2	14	3	2	11	4	6	5	2	6	2	6	19	49	49		1
42 cm	46	27	44	23	18	33	19	20	23	12	14	12	16	95	119	140	11	19
45 cm	291	318	280	143	210	315	127	85	129	97	56	105	65	457	362	604	104	147
48 cm	1,191	876	1,065	629	938	1,215	650	486	848	676	461	767	550	1,444	782	1,480	394	675
51 cm	2,099	936	1,555	971	1,457	1,458	1,352	1,054	1,562	1,589	1,378	1,517	1,370	2,043	1,049	1,624	739	905
54 cm	2,138	789	1,374	869	1,351	1,090	1,227	1,107	1,223	1,644	1,726	1,349	1,448	1,862	1,203	1,411	901	813
57 cm	1,784	758	932	689	983	698	859	868	798	1,176	1,458	1,036	993	1,306	1,264	1,332	906	521
60 cm	1,427	773	628	542	607	409	550	583	520	722	927	669	560	913	806	1,107	686	354
63 cm	910	630	424	327	344	257	316	354	380	451	552	439	332	521	411	651	672	238
66 cm	507	389	242	160	175	146	190	179	202	273	291	249	187	291	216	359	439	117
69 cm	255	209	128	74	66	60	116	90	112	149	153	111	87	172	108	181	260	52
72 cm	103	82	56	25	22	24	67	39	54	65	86	59	38	60	37	66	114	75
75 cm	36	32	13	9	5	5	28	12	13	28	30	27	10	22	14	14	34	12
78 cm	7	7	8		1	1	11	4	5	13	10	10	2	10	5	8	17	8
81 cm	2	2	2				1		2	2	2	1	1	2		1	2	
84 cm	1	1																
87 cm	1																	
Total	10,799	5,831	6,765	4,464	6,179	5,723	5,517	4,888	5,876	6,899	7,150	6,353	5,665	9,218	6,436	9,043	5,279	3,937

[1] Size groups by 3-cm. intervals.

TABLE 22.—*Size compositions of large haddock, fall seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
36 cm		1				1						1			6	3		
39 cm	14	4	6	4	1	12	4	2	5	1	6	4	3	6	49	22	3	2
42 cm	59	43	48	44	19	44	21	19	26	10	30	11	16	62	181	74	23	14
45 cm	233	545	401	213	324	337	203	199	362	90	156	129	109	436	406	346	126	132
48 cm	463	1,726	1,173	617	1,320	1,081	913	729	1,451	640	601	825	684	1,248	554	1,316	559	694
51 cm	852	1,802	1,585	944	1,770	1,605	1,327	1,043	1,978	1,326	1,145	1,361	1,267	1,771	820	2,047	1,005	959
54 cm	1,029	1,158	1,277	777	1,174	1,182	1,179	805	1,196	1,242	1,122	883	1,109	1,671	984	1,521	1,023	729
57 cm	1,089	716	762	584	712	600	788	486	505	776	752	438	713	1,217	936	996	797	531
60 cm	956	514	405	372	336	274	468	282	195	413	449	229	356	671	706	878	494	413
63 cm	722	392	223	210	166	138	228	149	116	210	221	124	193	327	387	613	360	272
66 cm	410	244	156	90	63	78	121	64	55	113	143	71	115	128	194	343	255	156
69 cm	171	110	67	37	24	38	70	28	19	53	54	42	50	55	118	164	131	93
72 cm	103	48	28	9	11	12	27	17	6	25	24	14	20	25	60	52	80	52
75 cm	49	12	10	5	6	5	11	7	8	10	16	5	12	9	23	20	16	20
78 cm	11	2	2	1	1	1	5	2	2	3	6	1	4	3	2	2	4	7
81 cm	2	1	3				1	1			1		2		1	2	2	1
84 cm	1		1												1			
Total	6,164	7,318	6,147	3,907	5,927	5,408	5,366	3,833	5,924	4,912	4,726	4,138	4,653	7,629	5,428	8,399	4,878	4,075

[1] Size groups by 3-cm. intervals.

TABLE 23.—*Size compositions of large haddock, winter seasons*

[In tbousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
30 cm															2			
33 cm		1													4			
36 cm		1								5				1	25			1
39 cm	6	2	1	1	1	1	1	4	2	18	1	1	2	7	48	5		3
42 cm	96	36	4	10	12	13	7	16	16	41	2	10	14	29	138	38	5	7
45 cm	410	276	39	87	216	119	49	90	124	64	36	55	68	90	314	137	51	94
48 cm	404	837	157	191	734	384	220	315	474	232	148	307	289	193	446	394	145	420
51 cm	420	911	257	229	748	431	355	451	734	448	356	536	432	459	322	598	257	486
54 cm	459	557	240	161	526	364	439	416	564	470	439	470	346	561	380	624	318	389
57 cm	422	396	179	98	376	265	406	318	374	310	371	298	219	569	461	528	310	326
60 cm	332	341	118	64	276	170	322	249	229	220	303	197	145	470	451	444	258	256
63 cm	229	258	86	36	222	116	249	182	165	146	201	118	86	279	327	354	198	198
66 cm	121	167	50	18	160	71	155	124	111	104	122	69	46	174	200	188	148	136
69 cm	67	67	26	10	82	37	90	71	57	51	70	36	30	99	101	100	101	81
72 cm	32	32	9	3	36	16	48	35	31	18	42	17	12	43	40	44	47	44
75 cm	8	9	5	4	8	5	20	12	10	12	18	11	6	12	19	16	17	15
78 cm		2	1		2	1	5	2	2	6	3	2	1	1	8	4	6	4
81 cm		1					1		1	2	2	1	2		1	1	1	1
84 cm										1								
Total	3,006	3,894	1,172	912	3,399	1,993	2,367	2,285	2,894	2,148	2,114	2,128	1,698	2,987	3,287	3,475	1,862	2,461

[1] Size groups by 3-cm. intervals.

TABLE 24.—*Size composition of large haddock, in each of the 18 years*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
30 cm															2	1		
33 cm		1													4	1		
36 cm		2				2		2		5		1		3	42	22	1	1
39 cm	27	9	21	9	4	25	11	16	14	22	13	8	15	39	149	96	6	6
42 cm	237	146	112	82	53	99	55	62	72	72	49	43	61	222	463	370	55	51
45 cm	1,190	1,418	901	510	794	860	497	412	651	363	299	364	315	1,131	1,194	1,531	377	418
48 cm	2,883	3,987	3,032	1,713	3,124	3,130	2,419	1,722	3,055	2,195	1,605	2,361	1,939	3,481	2,177	3,853	1,559	1,995
51 cm	4,769	4,333	4,471	2,554	4,215	4,271	4,259	3,074	4,962	4,534	3,904	4,359	4,027	5,341	2,864	4,877	2,947	2,876
54 cm	5,193	3,257	3,788	2,201	3,340	3,434	4,016	2,986	3,761	4,374	4,456	3,694	3,881	5,139	3,358	4,107	3,381	2,558
57 cm	4,832	2,704	2,626	1,688	2,304	2,231	2,950	2,271	2,392	2,945	3,521	2,596	2,611	3,824	3,389	3,309	2,984	1,968
60 cm	3,900	2,342	1,783	1,209	1,397	1,288	1,948	1,558	1,504	1,757	2,283	1,681	1,477	2,531	2,548	2,751	2,079	1,433
63 cm	2,603	1,777	1,183	726	872	817	1,205	991	1,077	1,048	1,337	1,063	863	1,410	1,475	1,846	1,775	1,054
66 cm	1,402	1,100	730	367	474	469	698	550	634	650	754	586	510	765	795	999	1,117	637
69 cm	625	534	339	168	210	222	398	281	355	341	378	283	234	410	414	491	614	388
72 cm	289	205	134	55	86	86	196	135	169	150	204	134	95	167	169	181	304	235
75 cm	111	69	35	24	22	25	76	50	57	60	87	57	36	59	71	59	74	66
78 cm	18	13	15	5	4	4	23	13	19	27	24	17	11	18	15	14	28	20
81 cm	4	4	5				3	1	5	5	6	2	5	2	2	4	5	3
84 cm	2	1	1						1	1					1			
87 cm	1																	
Total	28,086	21,902	19,176	11,311	16,899	16,963	18,754	14,124	18,692	18,549	18,920	17,249	16,080	24,542	19,132	24,512	17,306	13,709

[1] Size groups by 3-cm. intervals.

TABLE 25.—*Average size composition of large haddock, in each of the seasons*

[In thousands of fish]

Length [1]	Spring	Summer	Fall	Winter
36 cm		2	1	2
39 cm	3	10	8	6
42 cm	21	38	41	27
45 cm	126	216	264	129
48 cm	457	840	922	349
51 cm	828	1,370	1,367	468
54 cm	868	1,307	1,114	429
57 cm	731	1,020	744	346
60 cm	524	710	467	269
63 cm	356	456	281	192
66 cm	203	256	156	120
69 cm	100	132	74	65
72 cm	42	60	34	31
75 cm	14	19	14	12
78 cm	3	7	3	3
81 cm		1	1	1
Total	4,276	6,444	5,491	2,449

[1] Size groups by 3-cm. intervals.

TABLE 26.—*Size composition of large haddock in the average year*

[In thousands of fish]

Length [1]	Average number	Percent
36 cm	4	
39 cm	27	0.1
42 cm	128	.7
45 cm	735	3.9
48 cm	2,569	13.8
51 cm	4,032	21.7
54 cm	3,718	19.9
57 cm	2,841	15.2
60 cm	1,970	10.6
63 cm	1,285	6.9
66 cm	736	3.9
69 cm	371	2.0
72 cm	167	.9
75 cm	59	.3
78 cm	16	.1
81 cm	3	
Total	18,661	100.0

[1] Size groups by 3-cm. intervals.

TABLE 27.—*Size compositions of total haddock, spring seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
21 cm							1				1							
24 cm							1				3							
27 cm						1		2			13		1					
30 cm	1	7				28	9	30	9		108	5	12	2		9		
33 cm	1	31	2	2	1	74	40	113	37	16	555	33	63	11		15	10	2
36 cm	15	292	44	14	13	98	105	174	162	101	1,211	125	208	63	2	42	76	87
39 cm	62	928	172	63	68	153	280	189	462	296	1,121	386	778	257	33	117	385	531
42 cm	196	1,504	507	247	148	379	562	321	969	663	822	1,127	1,551	516	169	316	908	1,047
45 cm	431	1,390	1,009	415	207	739	984	558	1,267	1,101	1,235	2,023	1,740	762	342	632	995	970
48 cm	893	879	1,115	432	226	970	1,362	734	1,133	1,558	1,644	1,992	1,571	1,077	507	720	1,010	780
51 cm	1,412	723	1,176	434	268	894	1,440	779	886	1,482	1,558	1,438	1,399	1,213	686	613	1,117	699
54 cm	1,569	755	904	395	292	815	1,200	703	809	1,061	1,247	1,063	1,094	1,062	794	551	1,165	651
57 cm	1,537	834	753	317	233	674	901	610	717	688	944	825	722	735	730	453	971	590
60 cm	1,185	714	632	231	178	435	608	448	561	402	604	586	434	477	585	322	641	410
63 cm	742	497	450	153	140	306	412	307	416	241	363	382	260	283	350	228	545	346
66 cm	364	300	282	99	76	174	232	183	266	160	198	197	165	172	185	109	275	228
69 cm	132	148	118	47	38	87	122	92	167	88	101	94	68	84	87	46	122	162
72 cm	51	43	41	18	17	34	54	44	78	42	52	44	26	39	32	19	63	64
75 cm	18	16	7	6	3	10	17	19	26	10	23	14	8	16	15	9	7	19
78 cm		2	4	4		1	2	5	10	5	5	4	4	4			1	1
81 cm									2	1	1							1
84 cm									1									
Total	8,609	9,063	7,216	2,877	1,908	5,872	8,332	5,311	7,978	7,915	11,809	10,338	10,104	6,773	4,517	4,201	8,291	6,588

[1] Size groups by 3-cm. intervals.

TABLE 28.—*Size compositions of total haddock, summer seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
21 cm						1												
24 cm			14			2		1			2							
27 cm			152			5		3			4	1	1			11		
30 cm		1	290	2	1	19		16	1		15	10	24	4		29		
33 cm		16	373	12	13	128	17	62	25	9	163	106	214	10	29	211	17	52
36 cm	8	114	524	103	189	636	265	397	345	134	949	531	655	86	344	570	556	696
39 cm	75	661	650	228	625	1,561	1,123	1,281	1,064	589	2,052	1,232	1,282	461	917	989	1,366	1,759
42 cm	286	1,621	636	495	917	1,735	1,741	1,497	1,791	1,188	1,939	1,770	2,182	1,091	807	1,173	1,526	2,439
45 cm	615	2,125	873	893	1,238	1,680	1,470	1,065	2,177	1,524	1,458	2,829	2,319	1,557	623	1,976	1,353	2,488
48 cm	1,343	1,718	1,412	1,092	1,594	2,115	1,368	1,255	2,350	2,092	1,952	3,473	2,125	2,080	886	2,194	1,126	1,743
51 cm	2,116	1,095	1,647	854	1,611	1,716	1,570	1,321	1,967	2,153	2,071	2,402	1,909	2,155	1,066	1,728	916	1,040
54 cm	2,139	803	1,383	874	1,371	1,119	1,281	1,140	1,254	1,700	1,833	1,465	1,505	1,870	1,204	1,419	917	825
57 cm	1,784	758	933	690	987	701	895	873	804	1,180	1,472	1,046	1,001	1,306	1,264	1,332	906	521
60 cm	1,427	773	628	543	607	410	568	584	520	722	927	669	562	913	806	1,108	686	356
63 cm	910	630	424	327	344	257	318	354	380	451	552	439	332	521	411	652	672	238
66 cm	507	389	242	160	175	146	190	179	202	273	291	249	187	291	216	359	439	117
69 cm	255	209	128	74	66	60	116	90	112	149	153	111	87	172	108	181	260	52
72 cm	103	82	56	25	22	24	67	39	54	65	86	59	38	60	37	66	114	75
75 cm	36	32	13	9	5	5	28	12	13	28	30	27	10	22	14	14	34	12
78 cm	7	7	8		1	1	11	4	5	13	10	10	2	10	5	8	17	8
81 cm	2	2	2				1		2	2	2	1	1	2		1	2	
84 cm	1	1																
87 cm	1																	
Total	11,615	11,037	10,388	6,381	9,766	12,321	11,029	10,173	13,066	12,272	15,961	16,430	14,436	12,611	8,737	14,021	10,907	12,421

[1] Size groups by 3-cm. intervals.

TABLE 29.—*Size compositions of total haddock, fall seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
24 cm							2				1							
27 cm			1			4	30			6	10	1			1	1		
30 cm	1		17	2	1	17	166	1	1	48	59	5	3	3	6	8	4	4
33 cm	7	1	44	41	24	103	383	40	43	183	136	58	41	50	12	36	54	104
36 cm	127	30	254	362	256	346	385	370	354	242	664	649	337	139	180	270	1,122	1,076
39 cm	750	322	1,234	1,098	1,311	1,310	1,054	2,293	1,596	415	2,525	1,905	839	321	861	906	4,253	2,160
42 cm	1,358	1,590	1,991	1,140	2,192	2,734	2,465	4,606	3,288	1,201	4,576	2,305	1,237	794	1,425	1,570	4,505	2,403
45 cm	1,010	3,137	1,522	906	1,972	2,509	2,598	3,558	3,540	1,625	3,336	1,914	1,662	1,365	1,204	1,850	2,331	2,394
48 cm	666	3,088	1,546	1,002	1,980	1,857	1,907	1,821	2,997	1,716	1,707	1,920	1,846	1,666	767	2,114	1,480	1,935
51 cm	880	2,005	1,638	1,011	1,881	1,745	1,515	1,220	2,286	1,673	1,422	1,625	1,548	1,848	852	2,211	1,152	1,195
54 cm	1,036	1,179	1,278	778	1,181	1,196	1,198	830	1,223	1,289	1,157	917	1,133	1,685	1,000	1,532	1,047	761
57 cm	1,090	718	762	585	712	602	788	489	508	779	754	441	715	1,219	938	996	801	537
60 cm	956	514	405	372	336	274	468	282	195	414	449	229	356	671	706	878	494	415
63 cm	722	392	223	210	166	138	228	149	116	210	221	124	193	327	387	613	360	272
66 cm	410	244	156	90	63	78	121	64	55	113	143	71	115	128	194	343	255	156
69 cm	171	110	67	37	24	38	70	28	19	53	54	42	50	55	118	164	131	93
72 cm	103	48	28	9	11	12	27	17	6	25	24	14	20	25	60	52	80	52
75 cm	49	12	10	5	6	5	11	7	8	10	16	5	12	9	23	20	16	20
78 cm	11	2	2	1	1	1	5	2	2	3	6	1	4	3	2	2	4	7
81 cm	2	1	3				1	1			1		2		1	2	2	1
84 cm	1		1												1			
Total	9,350	13,393	11,182	7,649	12,117	12,969	13,422	15,778	16,237	10,005	17,261	12,226	10,113	10,308	8,738	13,568	18,091	13,585

[1] Size groups by 3-cm. intervals.

TABLE 30.—*Size compositions of total haddock, winter seasons*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
24 cm					2													
27 cm				16	11	5	2	4	2	1	7	1						
30 cm	1			80	140	37	18	67	28	63	55	10			2	3		4
33 cm	34	2	14	109	485	168	74	243	135	321	114	49	5	5	11	24	32	105
36 cm	694	20	68	176	632	343	149	418	434	571	169	204	63	29	62	107	254	894
39 cm	2,060	154	190	293	644	363	156	648	721	437	404	780	201	59	240	335	813	1,715
42 cm	2,360	603	366	399	1,001	473	217	1,215	842	329	1,078	1,361	288	108	586	699	883	1,544
45 cm	1,615	1,121	270	291	1,561	684	444	1,266	1,011	514	1,448	1,131	349	281	771	732	495	1,226
48 cm	678	1,282	220	235	1,452	634	512	796	984	616	846	830	497	300	566	690	322	996
51 cm	439	970	265	235	884	467	434	556	850	561	512	668	472	467	333	672	299	620
54 cm	460	563	241	161	537	369	448	427	576	487	465	484	353	561	381	638	321	406
57 cm	423	396	179	98	377	266	407	320	375	311	372	299	220	569	461	531	311	329
60 cm	332	341	118	64	276	170	322	249	229	220	303	197	145	470	451	445	258	256
63 cm	229	258	86	36	222	116	249	182	165	146	201	118	86	279	327	354	198	198
66 cm	121	167	50	18	160	71	155	124	111	104	122	69	46	174	200	188	148	136
69 cm	67	67	26	10	82	37	90	71	57	51	70	36	30	99	101	100	101	81
72 cm	32	32	9	3	36	16	48	35	31	18	42	17	12	43	40	44	47	44
75 cm	8	9	5	4	8	5	20	12	10	12	18	11	6	12	19	16	17	15
78 cm		2	1		2	1	5	2	2	6	3	2	1	1	8	4	6	4
81 cm		1					1		1	2	2	1	2		1	1	1	1
84 cm										1								
Total	9,553	5,988	2,108	2,228	8,512	4,225	3,751	6,635	6,564	4,771	6,231	6,268	2,776	3,457	4,560	5,583	4,506	8,574

[1] Size groups by 3-cm. intervals.

TABLE 31.—*Size composition of landings of total haddock, in each of the 18 years*

[In thousands of fish]

Length [1]	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
21 cm						1	1				1							
24 cm			14		2	2	3	1			6							
27 cm			153	16	11	15	32	9	2	7	34	3	2		1	12		
30 cm	3	8	307	84	142	101	193	114	39	111	237	30	39	9	8	49	4	8
33 cm	42	50	433	164	523	473	514	458	240	529	968	246	323	76	52	286	113	263
36 cm	844	456	890	655	1,090	1,423	904	1,359	1,295	1,048	2,993	1,509	1,263	317	588	989	2,008	2,753
39 cm	2,947	2,065	2,246	1,682	2,648	3,387	2,613	4,411	3,843	1,737	6,102	4,303	3,100	1,098	2,051	2,347	6,817	6,165
42 cm	4,200	5,318	3,500	2,281	4,258	5,321	4,985	7,639	6,890	3,381	8,415	6,563	5,258	2,509	2,987	3,758	7,822	7,433
45 cm	3,671	7,773	3,674	2,505	4,978	5,612	5,496	6,447	7,995	4,764	7,477	7,897	6,070	3,965	2,940	5,190	5,174	7,078
48 cm	3,580	6,967	4,293	2,761	5,252	5,576	5,149	4,606	7,464	5,982	6,149	8,125	6,039	5,123	2,726	5,718	3,938	5,454
51 cm	4,847	4,793	4,726	2,734	4,644	4,822	4,959	3,876	5,989	5,869	5,563	6,133	5,328	5,683	2,937	5,224	3,484	3,554
54 cm	5,204	3,300	3,806	2,208	3,381	3,499	4,127	3,100	3,862	4,537	4,702	3,929	4,085	5,178	3,379	4,140	3,450	2,643
57 cm	4,834	2,706	2,627	1,690	2,309	2,243	2,991	2,292	2,404	2,958	3,542	2,611	2,658	3,829	3,393	3,312	2,989	1,977
60 cm	3,900	2,342	1,783	1,210	1,397	1,289	1,966	1,563	1,505	1,758	2,283	1,681	1,497	2,531	2,548	2,753	2,079	1,437
63 cm	2,603	1,777	1,183	726	872	817	1,207	992	1,077	1,048	1,337	1,063	871	1,410	1,475	1,847	1,775	1,054
66 cm	1,402	1,100	730	367	474	469	698	550	634	650	754	586	513	765	795	999	1,117	637
69 cm	625	534	339	168	210	222	398	281	355	341	378	283	235	410	414	491	614	388
72 cm	289	205	134	55	86	86	196	135	169	150	204	134	96	167	169	181	304	235
75 cm	111	69	35	24	22	25	76	50	57	60	87	57	36	59	71	59	74	66
78 cm	18	13	15	5	4	4	23	13	19	27	24	17	11	18	15	14	28	20
81 cm	4	4	5				3	1	5	5	6	2	5	2	2	4	5	3
84 cm	2	1	1						1	1					1			
87 cm	1																	
Total	39,127	39,481	30,894	19,335	32,303	35,387	36,534	37,897	43,845	34,963	51,262	45,262	37,429	33,149	26,552	37,373	41,795	41,168

[1] Size groups by 3-cm. intervals.

TABLE 32.—*Average size composition of total [1] haddock, in each of the seasons*

[In thousands of fish]

Length [2]	Spring	Summer	Fall	Winter
24 cm		1		
27 cm	1	10	3	3
30 cm	12	23	19	28
33 cm	56	81	76	107
36 cm	157	395	398	294
39 cm	349	995	1,397	567
42 cm	664	1,380	2,299	797
45 cm	933	1,570	2,135	844
48 cm	1,035	1,773	1,779	692
51 cm	1,012	1,641	1,539	539
54 cm	896	1,339	1,134	438
57 cm	735	1,025	746	347
60 cm	525	712	467	269
63 cm	357	456	281	192
66 cm	204	256	156	120
69 cm	100	132	74	65
72 cm	42	60	34	31
75 cm	14	19	14	12
78 cm	3	7	3	3
81 cm		1	1	1
Total	7,095	11,876	12,555	5,349

[1] All values calculated by dividing 18-year total for total haddock by 18 rather than by summing 18-year averages of scrod plus large.
[2] Size groups by 3-cm. intervals.

TABLE 33.—*Size composition of total haddock in the average year*

[In thousands of fish]

Length [1]	Average number	Percent
24 cm	1	
27 cm	17	0.1
30 cm	82	.2
33 cm	320	.9
36 cm	1,244	3.4
39 cm	3,308	9.0
42 cm	5,140	13.9
45 cm	5,482	14.9
48 cm	5,279	14.3
51 cm	4,731	12.8
54 cm	3,807	10.3
57 cm	2,853	7.7
60 cm	1,973	5.4
63 cm	1,286	3.5
66 cm	736	2.0
69 cm	371	1.0
72 cm	167	.4
75 cm	59	.2
78 cm	16	
81 cm	3	
Total	36,875	100.0

[1] Size groups by 3-cm. intervals.

TABLE 34.—*Undersized haddock landed, by years*

[In thousands of fish]

Year	Number of fish
1931	3,836
1932	2,579
1933	4,043
1934	2,601
1935	4,416
1936	5,402
1937	4,260
1938	6,352
1939	5,419
1940	3,432
1941	10,341
1942	6,091
1943	4,727
1944	1,500
1945	2,700
1946	3,683
1947	8,942
1948	9,189
Total	89,513
Average	4,974

TABLE 35.—*Division of landings for each size*

Length [1]	Percent of landings	
	Scrod	Large
33 cm. and under	100.0	
36 cm	99.7	0.3
39 cm	99.2	.8
42 cm	97.5	2.5
45 cm	86.6	13.4
48 cm	51.3	48.7
51 cm	14.8	85.2
54 cm	2.3	97.7
57 cm	.4	99.6
60 cm	.2	99.8
63 cm	.1	99.9
66 cm. and over		100.0
All sizes	49.4	50.6

[1] Size groups by 3-cm. intervals.

DISCUSSION AND SUMMARY

1. Presented in this paper is an outline of a study of Georges Bank haddock and also details of landings for the years of 1931 to 1948. Pounds, numbers, and average weights of fish, and size compositions of landings are given for scrod, for large, and for total haddock. While these data are presented primarily as background for further studies, the averages and ranges are informative. The values presented, in our opinion, are as nearly complete a record of the quantities of Georges Bank haddock that were landed and sold as can be readily assembled. They are more nearly complete than values previously given (Schuck 1949), which represent only Georges Bank haddock landed at the ports of Boston, Gloucester, and New Bedford, Mass., and Portland, Maine.

2. The industry is most affected, not by the average or ordinary condition of the fishery, but by deviations from the normal, be it in terms of pounds of fish, of numbers of fish, of numbers of certain sizes as compared with previous years, or of a change in the seasonal cycle of the above. But, in order to measure deviations, it is first necessary to determine the norm from which they deviate. We can define the average year as follows: In the average year (during the period 1931–1948) there were 94,196,000 pounds of haddock (30,791,000 pounds of scrod and 63,405,000 pounds of large) landed from Georges Bank. The average weight of these fish was 2.55 pounds (1.69 for scrod, 3.40 for large) and 36,875,000 individual fish (18,214,000 scrod and 18,661,000 large) were landed. Of these numbers landed, there were practically none less than 27 centimeters (9.6 inches), and none more than 81 centimeters (32.1 inches) in length. The 45-centimeter (17.9-inch)

group contained the most fish and over 66 percent of all haddock landed were between the 42-centimeter (16.2-inch) group and the 54-centimeter (22.1-inch) group in length.

Also in the average year about 4,974,000 fish or 13.5 percent of the total number landed were smaller than the established minimum market size of 1½ pounds.

3. So far as subareas of Georges Bank are concerned, in the average year (1936 to 1948 only) the Northern Edge, though not the largest area, has been the largest producer, with 35 percent of the total poundage.

Percentages for scrod, large, and total haddock from the four areas are as follows:

	Scrod	*Large*	*Total haddock*
Northern Edge	39. 5	32. 9	35. 2
Southeast Part	26. 3	23. 3	24. 4
South Channel	28. 6	36. 4	33. 6
Southwest Part	5. 6	7. 4	6. 8
	100. 0	100. 0	100. 0

4. The seasonal landings, for the average year, are shown in table 36 by pounds, numbers, and average weights.

TABLE 36.—*Seasonal average weights and quantities landed*

	Pounds of fish (thousands)	Number of fish (thousands)	Average weight per fish (pounds)
Spring:			
Scrod	5, 273	2, 819	1. 871
Large	15, 899	4, 276	3. 718
Total	21, 172	7, 095	2. 984
Summer:			
Scrod	8, 448	5, 430	1. 556
Large	20, 389	6, 444	3. 163
Total	28, 837	11, 876	2. 430
Fall:			
Scrod	12, 147	7, 064	1. 719
Large	18, 152	5, 491	3. 306
Total	30, 299	12. 555	2. 413
Winter:			
Scrod	4, 923	2, 901	1. 697
Large	8, 965	2, 449	3. 661
Total	13, 888	5, 349	2. 596
Year:			
Scrod	30, 791	18, 214	1. 691
Large	63, 405	18, 660	3. 398
Total	94, 196	36, 875	2. 554

From table 36, we have computed the percent by weight and the percent by number for scrod, large, and total haddock of the year's landings. They are as follows:

	By weight	*By number*
Scrod:		
Spring	17. 1	15. 5
Summer	27. 4	29. 8
Fall	39. 5	38. 8
Winter	16. 0	15. 9
Total year	100. 0	100. 0
Large:		
Spring	25. 1	22. 9
Summer	32. 2	34. 6
Fall	28. 6	29. 4
Winter	14. 1	13. 1
Total year	100. 0	100. 0
Total haddock:		
Spring	22. 5	19. 2
Summer	30. 6	32. 2
Fall	32. 2	34. 1
Winter	14. 7	14. 5
Total year	100. 0	100. 0

Landings of undersized haddock were greatest in the fall season, when 38 percent of the yearly average landings of undersized fish occurred. The summer season accounted for 30 percent, the winter season for 20 percent, and the spring season for the least quantity, 12 percent. Considering each season separately, the percentages of haddock landed that were undersized are as follows:

	Percent undersized
Spring	8. 1
Summer	12. 7
Fall	15. 1
Winter	18. 7
Total year	13. 5

5. Having thus developed average values of important characteristics of the landings, each individual year can be evaluated by comparing it with these norms. For instance, considering 1934 (the poorest year of haddock production), we see that only 12,976,000 pounds of scrod as compared with the average of 30,791,000 pounds were landed; only 36,908,000 pounds of large haddock as compared with the average of 63,405,000; and only 49,884,000 pounds of all haddock as compared with the average of 94,196,000. Average weights for 1934 as compared to the average year were:

	1934	*Average year*
Scrod	1. 62	1. 69
Large	3. 26	3. 40
Total haddock	2. 58	2. 55

The numbers of fish landed in 1934 as compared with 18-year averages were: scrod 8,024,000 (18,214,000), large 11,311,000 (18,661,000), total haddock 19,335,000 (36,875,000).

In addition to such yearly deviations, seasonal deviations for 1934 can be compared with average seasonal values, and subarea contributions can be evaluated in terms of average subarea contributions.

6. For a rapid evaluation of how each of the 18 years deviate in the more important characteristics from the average year, table 37 has been prepared. Shown are the percentages that the individual years are above or below the 18-year average; pounds, numbers, and average weights are treated, for large, scrod and total haddock.

7. The data in this paper serve (1) as a record of the total landings of haddock from Georges Bank in terms of pounds, average weights, numbers and sizes of scrod, large, and total haddock, by seasons and years over the 18-year period, 1931 to 1948; and (2) as a basis for developing other data, among which will be the age composition of the landings; the size of various ages; year class contributions; and estimates of the relative size of the stock on the banks, of rates of decline of year classes, and of mortality rates.

TABLE 37.—*Percentage deviations of quantities and average weights from the average year*

	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948
Pounds:																		
Scrod	−43.2	2.3	−38.9	−57.9	−17.1	−2.7	1.0	29.6	40.1	−3.9	74.6	60.7	21.8	−50.5	−62.1	−31.4	32.8	44.7
Large	53.8	16.6	−.9	−41.8	−15.4	−14.7	1.5	−17.2	−3.2	−.6	7.2	−9.1	−17.9	27.4	5.0	30.5	1.5	−22.8
Total	22.1	11.9	−13.3	−47.0	−15.9	−10.8	1.3	−1.9	11.0	−1.6	29.2	13.7	−4.9	1.9	−16.9	10.3	11.8	−.7
Numbers:																		
Scrod	−39.4	−3.5	−35.7	−55.9	−15.4	1.2	−2.4	30.5	38.1	−9.9	77.6	53.8	17.2	−52.8	−59.3	−29.4	34.4	50.8
Large	50.5	17.4	2.8	−39.4	−9.4	−9.1	.5	−24.3	.2	−.6	1.4	−7.6	−13.8	31.5	2.5	31.4	−7.3	−26.5
Total	6.1	7.1	−16.2	−47.6	−12.4	−4.0	−.9	2.8	18.9	−5.2	39.0	22.7	1.5	−10.1	−28.0	1.4	13.3	11.6
Average weights (pounds):																		
Scrod	−6.2	6.0	−5.1	−4.3	−1.9	−3.8	3.4	−.7	1.4	6.7	−1.7	4.5	3.9	4.8	−6.9	−2.9	−1.2	−4.0
Large	2.2	−.7	−3.6	−4.0	−6.6	−6.2	1.0	9.4	−3.3	0	5.7	−1.7	−4.7	−3.2	2.5	−.6	9.4	5.1
Total	15.1	4.5	3.4	1.0	−4.0	−7.1	2.3	−4.5	−5.7	3.7	−7.0	−7.4	−6.3	13.4	15.4	8.8	−1.4	−11.1

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

COMPARISON OF HADDOCK FROM GEORGES AND BROWNS BANKS

By HOWARD A. SCHUCK and EDGAR L. ARNOLD, JR.

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CONTENTS

	Page
Collection of data	179
Size composition	179
Sizes at various ages	180
Summary	185
Literature cited	185

COMPARISON OF HADDOCK FROM GEORGES AND BROWNS BANKS

By HOWARD A. SCHUCK and EDGAR L. ARNOLD, JR., *Fishery Research Biologists*

Two large areas in the Northwest Atlantic Ocean are of utmost importance to the United States haddock fishery. These are the Georges Bank area and the chain of Nova Scotian banks. From these two areas comes over 95 percent of the United States production of haddock. In the years 1931 to 1949, the Georges Bank area produced about 2,092,000,000 pounds (round weight) of haddock and the Nova Scotian banks better than 910,000,000 pounds.

These two areas are close geographically but are separated by the relatively deep Fundian Channel. The question of the effectiveness of this channel as a barrier to the passage of haddock (*Melanogrammus aeglefinus*) between the Georges Bank area and the group of Nova Scotian banks is economically and scientifically important. Its answer, among other things, determines whether the haddock stocks in the two areas can be expected to fluctuate simultaneously or whether they must be considered separately in interpreting observed fluctuations in abundance.

It is possible that some intermingling of the egg or fry stages may occur between the two banks. Walford (1938), however, concluded that during 1931 and 1932 (the only years in which the drift of young has been studied) Georges Bank, at least, had received no recruits from other areas.

Regarding the bottom-dwelling stages of haddock, various investigators (Needler 1930, Herrington 1944) expressed the opinion that intermigration between the two areas is negligible, and that the populations inhabiting the two areas are largely independent. At present, direct evidence from the movement of marked fish is limited. Returns from haddock tagged in shallow inshore waters have been obtained (Needler 1930, Schroeder 1942, Rounsefell 1942, United States Fish and Wildlife Service unpublished records), but early tagging of large groups of haddock located off shore was unsuccessful. The extremely delicate haddock require special methods of collecting and handling, particularly in deep water, if returns are to be obtained. Recent attempts at offshore tagging from the *Albatross III* are proving successful, but it will be some time before enough returns are available to determine how much migration occurs across the Fundian Channel.

As for indirect lines of evidence, Vladykov (1935) has shown small differences in the average numbers of vertebrae in haddock from Georges Bank and the Nova Scotian banks. The significance of the differences is not known, as no measures of variation of these averages were given. Other data by Needler (1930) indicate differences in the size composition and the growth rate between Nova Scotian and Georges Bank haddock. But again only averages were given and the samples were taken by commercial gear which excluded the younger ages and possibly exercised selection for the larger sizes of certain ages.

Recent data collected on a cruise of the *Albatross III*, research vessel of the United States Fish and Wildlife Service, make possible a critical comparison between the haddock from Georges Bank and those from Browns Bank, the Nova Scotian bank lying closest to Georges. By such a comparison, it is the purpose of this report to consider further the effectiveness of the Fundian Channel as a barrier to bottom-dwelling stages of haddock. In effect, this study supplements Needler (1930) by including younger fish and by providing stringent statistical comparison of data from the two banks.

In collecting the original data for this study John B. Colton, Jr., Frank A. Dreyer, Freeman A. Pluff, Louis D. Stringer, and Roland L. Wigley assisted. Sterling L. Cogswell and Richard E. Sayles prepared the scales for study, and Manuel Vieira prepared the illustrations. Robert Kirkpatrick summarized the 1950 Browns Bank data, and John C. Marr, Chief, South Pacific Fishery Investigations, reviewed the manuscript.

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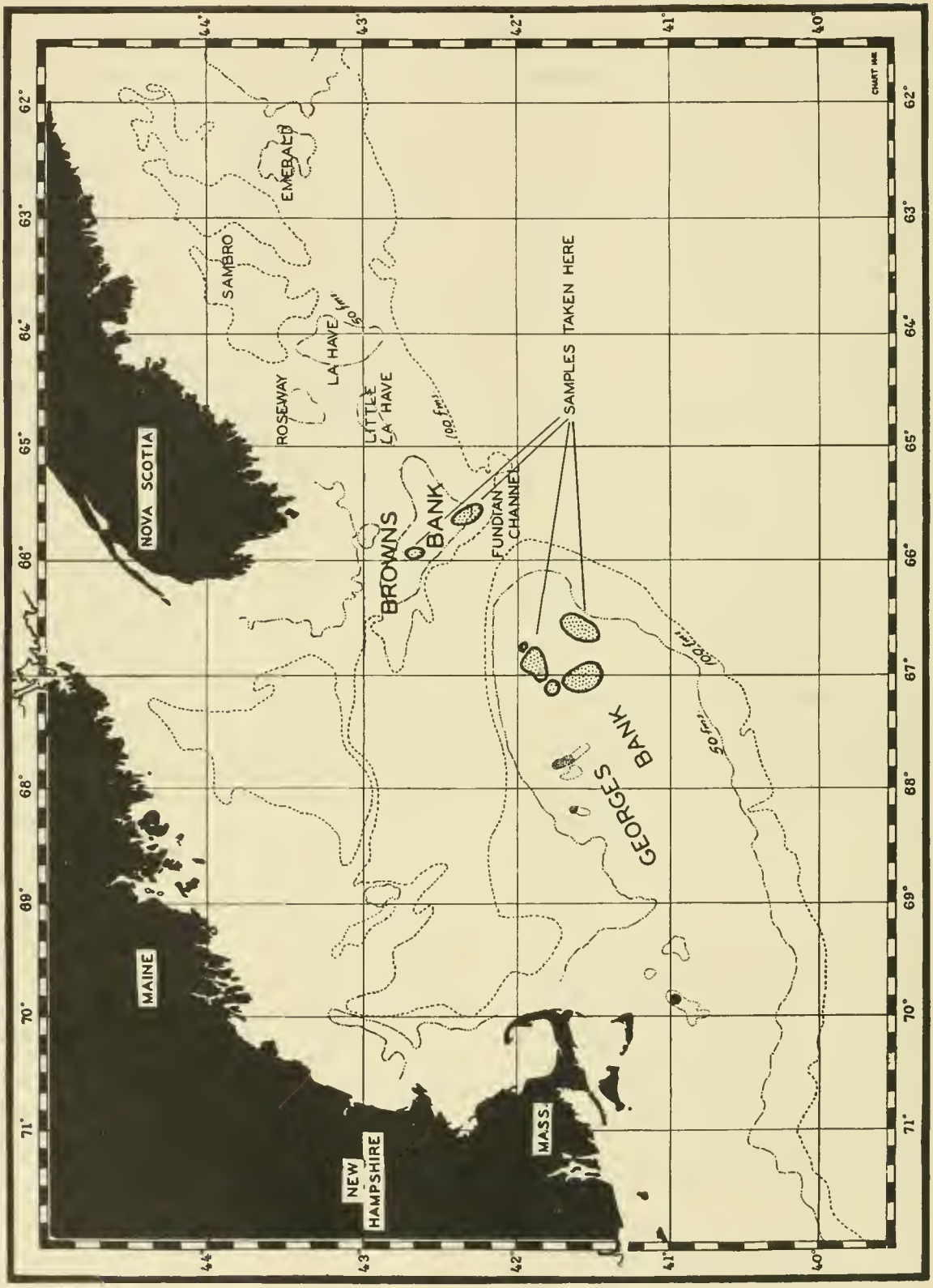

FIGURE 1.—Areas of Georges and Browns Banks from which sample haddock were taken.

COLLECTION OF DATA

Cruise 23 (June 23 to June 29, 1949) of the *Albatross III* was made primarily to tag haddock on Georges and Browns Banks. However, length measurements and scale samples were obtained concurrently from a substantial number of fish on each of the two banks, and these data form the basis for this report.

The mesh in the otter trawl used was small enough, 2-inch stretched measure, to obtain a representative sample of all sizes and ages of bottom-dwelling haddock (other than young of the year) in a given area. The samples were obtained from two locations on Browns Bank and from five locations on Georges Bank (fig. 1). These locations were not selected at random, but all fish caught on the two banks were taken in nets of the same size, fished in the same manner.

SIZE COMPOSITION

During this cruise, 10,163 haddock were caught in 61 tows, 9,321 in 45 tows on Georges Bank and 842 in 16 tows on Browns Bank. The size compositions[1] of these catches are shown in table 1. The percentage size compositions of the catches from the two banks also are shown in table 1 and are plotted in figure 2. From these data it can be seen that there is a marked difference in the size compositions of the catches from the two banks.

[1] By fork length, from tip of snout to fork of tail. All lengths were recorded by centimeters, that is, lengths from 20.0 centimeters to and including 20.9 centimeters were recorded as 20.0 centimeters, lengths from 21.0 centimeters to and including 21.9 centimeters were recorded as 21.0 centimeters, and so on. Data are arranged in 3-centimeter groups, that is, 20-, 21-, and 22-centimeter fish are grouped as 21-centimeter fish; 23-, 24-, and 25-centimeter fish are grouped as 24-centimeter fish, and so on.

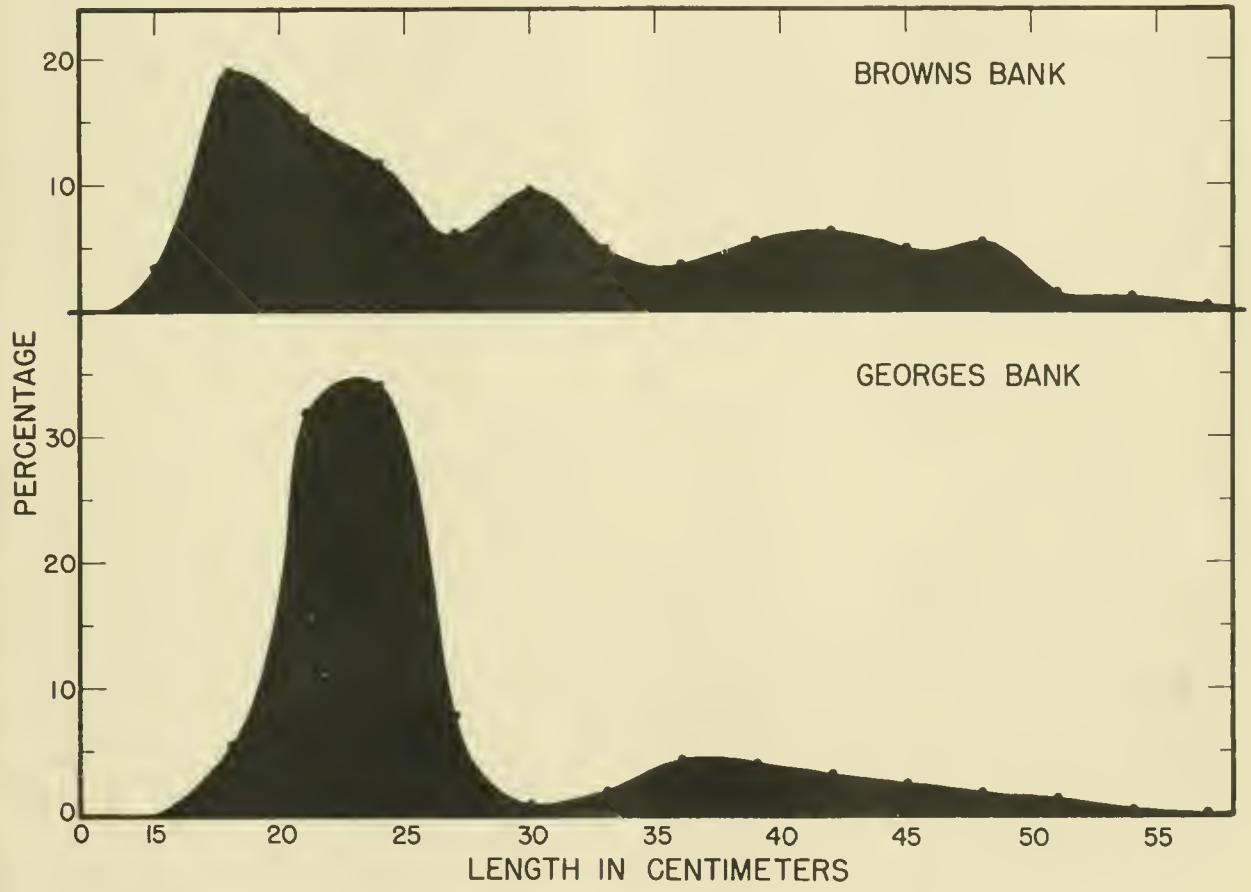

FIGURE 2.—Percentage size compositions of haddock catches from Georges and Browns Banks.

TABLE 1.—*Size compositions of haddock catches from Georges and Browns Banks*

Length in 3-centimeter groups [1]	Georges Bank		Browns Bank	
	Number	Percent	Number	Percent
15 centimeters			29	3.44
18 centimeters	511	5.48	160	19.00
21 centimeters	2,973	31.90	129	15.32
24 centimeters	3,180	34.12	99	11.76
27 centimeters	734	7.87	52	6.18
30 centimeters	75	.81	81	9.62
33 centimeters	182	1.95	41	4.87
36 centimeters	410	4.40	32	3.80
39 centimeters	376	4.03	47	5.58
42 centimeters	298	3.20	53	6.29
45 centimeters	239	2.56	42	4.99
48 centimeters	159	1.71	46	5.46
51 centimeters	117	1.26	12	1.42
54 centimeters	40	.43	10	1.19
57 centimeters	18	.19	4	.48
60 centimeters	3	.03	4	.48
63 centimeters	3	.03	1	.12
66 centimeters	1	.01		
69 centimeters				
72 centimeters	2	.02		
Total	9,321	100.00	842	100.00

[1] See text footnote 1.

SIZES AT VARIOUS AGES

Without some method of age determination, we could only speculate about the ages of the fish represented by the modes in these size distributions. Fortunately the age of haddock, at least for the ages represented here, can be assessed accurately by microscopic examination of impressions of their scales. Figure 3 shows impressions of scales of 1-, 2-, 3-, and 4-year-old haddock collected on this cruise.

Scale samples were taken from 1,285 haddock, 823 from Georges Bank and 462 from Browns Bank. Tables 2 and 3 show the distribution of these fish by size, and the number and percentage of fish from each size group that were assigned to each age on the basis of scale examination. From the percentages thus obtained, it was possible to estimate how many fish in the total catch were of each age.

It was necessary to determine the number of each age in the entire catch, rather than to use only the age samples of tables 2 and 3, because scales were taken from more large fish than from small, in proportion to their abundance. This was done because of the relative scarcity of larger sizes and because of the greater number of ages that make up the size groups of larger fish.

The age composition of the total catch was obtained by allotting the total catch of each size group (table 1) to the various ages on the basis of the percentages shown in tables 2 and 3. For example, the Georges Bank age analysis showed that, of all 18-centimeter fish for which age readings were made, 100 percent were 1-year olds. Accordingly, the total catch (511) of 18-centimeter haddock taken on Georges Bank were considered to be 1-year-old fish. Likewise, of all 36-centimeter fish for which the ages were read, 92.1 percent were 2-year-olds and 7.9 percent were 3-year-olds. Thus, of the 410 fish of 36

TABLE 2.—*Age composition of 823 Georges Bank haddock, by scale analysis*

[In parentheses is the percentage that each age contributed to the total for each size]

Length in 3-centimeter groups [1]	Number and percent in age group—									Total number, all ages
	1	2	3	4	5	6	7	8	9 and over	
18 centimeters	3 (100.0)									3
21 centimeters	39 (100.0)									39
24 centimeters	39 (100.0)									39
27 centimeters	18 (100.0)									18
30 centimeters	6 (46.2)	7 (53.8)								13
33 centimeters		65 (100.0)								65
36 centimeters		139 (92.1)	12 (7.9)							151
39 centimeters		105 (67.7)	50 (32.3)							155
42 centimeters		34 (30.6)	75 (67.6)	2 (1.8)						111
45 centimeters		2 (2.2)	69 (77.6)	18 (20.2)						89
48 centimeters			35 (56.4)	23 (37.1)	4 (6.5)					62
51 centimeters			10 (20.4)	35 (71.4)	4 (8.2)					49
54 centimeters				11 (78.6)	2 (14.3)	1 (7.1)				14
57 centimeters				3 (37.5)	3 (37.5)	1 (12.5)		1 (12.5)		8
60 centimeters					1 (50.0)	1 (50.0)				2
63 centimeters						2 (100.0)				2
66 centimeters						1 (100.0)				1
69 centimeters										0
72 centimeters								1 (50.0)	1 (50.0)	2
All sizes	105	352	251	92	14	6		2	1	823

[1] See text footnote 1.

TABLE 3.—*Age composition of 462 Browns Bank haddock, by scale analysis*

[In parentheses is the percentage that each age contributed to the total for each size]

Length in 3-centimeter groups [1]	Number and percent in age group—									Total number, all ages
	1	2	3	4	5	6	7	8	9 and over	
15 centimeters	13 (100.0)									13
18 centimeters	62 (89.9)	7 (10.1)								69
21 centimeters	13 (16.0)	68 (84.0)								81
24 centimeters		50 (96.2)	2 (3.8)							52
27 centimeters		11 (31.4)	24 (68.6)							35
30 centimeters			49 (100.0)							49
33 centimeters			32 (97.0)	1 (3.0)						33
36 centimeters			12 (63.2)	7 (36.8)						19
39 centimeters				19 (90.5)	2 (9.5)					21
42 centimeters				20 (87.0)	3 (13.0)					23
45 centimeters				10 (40.0)	15 (60.0)					25
48 centimeters				4 (17.4)	16 (69.6)	2 (8.7)	1 (4.3)			23
51 centimeters					5 (83.3)	0 (0.0)	1 (16.7)			6
54 centimeters					1 (12.5)	5 (62.5)	2 (25.0)			8
57 centimeters							1 (50.0)	1 (50.0)		2
60 centimeters								1 (100.0)		1
63 centimeters									2 (100.0)	2
All sizes	88	136	119	61	42	7	5	2	2	462

[1] See text footnote 1.

centimeters caught on Georges Bank, 378 (92.1 percent) were estimated to be 2-year-olds and 32 (7.9 percent) to be 3-year-olds.

The total numbers of haddock caught of each size and age, shown in tables 4 and 5, were transformed into percentages and plotted in figure 4. In effect, this amounted to converting the percentage size compositions shown in figure 2 into percentage age compositions. From figure 4, it can be seen that, as already suspected from figure 2, the modes are composed largely of fish of different ages.

It can be seen from figure 3 and also from table 6 that for each age the fish caught on Georges Bank were considerably larger than those caught on Browns Bank. One-year-olds from Georges averaged 22.7 centimeters as compared with only 17.9 centimeters from Browns; 2-year-olds from Georges were 36.6 centimeters as compared with 22.4 from Browns; 3-year-olds were 43.2 centimeters as compared with 30.6; 4-year-olds were 49.4 centimeters as compared with 41.1 centimeters. Also shown in table 6 are the ranges of the means, expressed as the mean + 2 times its standard

TABLE 4.—*Estimated age distribution of haddock catch from Georges Bank*

Length in 3-centimeter groups [1]	Number in age group—									Total, all ages
	1	2	3	4	5	6	7	8	9 and over	
18 centimeters	511									511
21 centimeters	2,973									2,973
24 centimeters	3,180									3,180
27 centimeters	734									734
30 centimeters	35	40								75
33 centimeters		182								182
36 centimeters		378	32							410
39 centimeters		255	121							376
42 centimeters		91	202	5						298
45 centimeters		5	186	48						239
48 centimeters			90	59	10					159
51 centimeters			24	83	10					117
54 centimeters				31	6	3				40
57 centimeters				7	7	2		2		18
60 centimeters					2	1				3
63 centimeters						3				3
66 centimeters						1				1
69 centimeters										0
72 centimeters							1	1		2
All sizes	7,433	951	655	233	35	10	0	3	1	9,321

[1] See text footnote 1.

TABLE 5.—*Estimated age distribution of haddock catch from Browns Bank*

Length in 3-centimeter groups [1]	Number in age group—									Total, all ages
	1	2	3	4	5	6	7	8	9 and over	
15 centimeters	29									29
18 centimeters	144	16								160
21 centimeters	21	108								129
24 centimeters		95	4							99
27 centimeters		16	36							52
30 centimeters			81							81
33 centimeters			40	1						41
36 centimeters			20	12						32
39 centimeters				42	5					47
42 centimeters				46	7					53
45 centimeters				17	25					42
48 centimeters				8	32	4	2			46
51 centimeters					10	0	2			12
54 centimeters					1	6	3			10
57 centimeters							2	2		4
60 centimeters								4		4
63 centimeters									1	1
All sizes	194	235	181	126	80	10	9	6	1	842

[1] See text footnote 1.

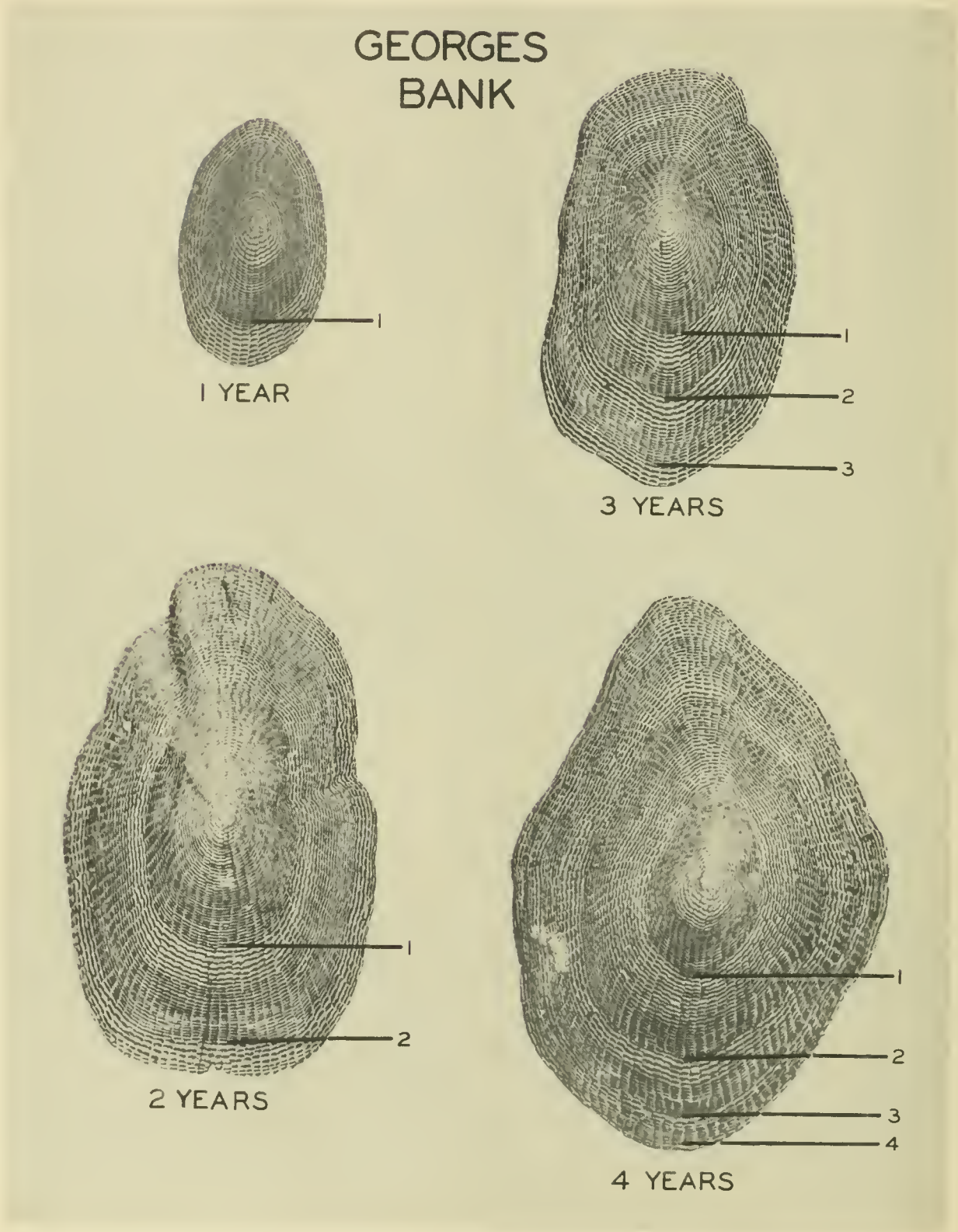

FIGURE 3a.—Impressions of scales of 1-, 2-, 3-, and 4-year old haddock from Georges Bank.

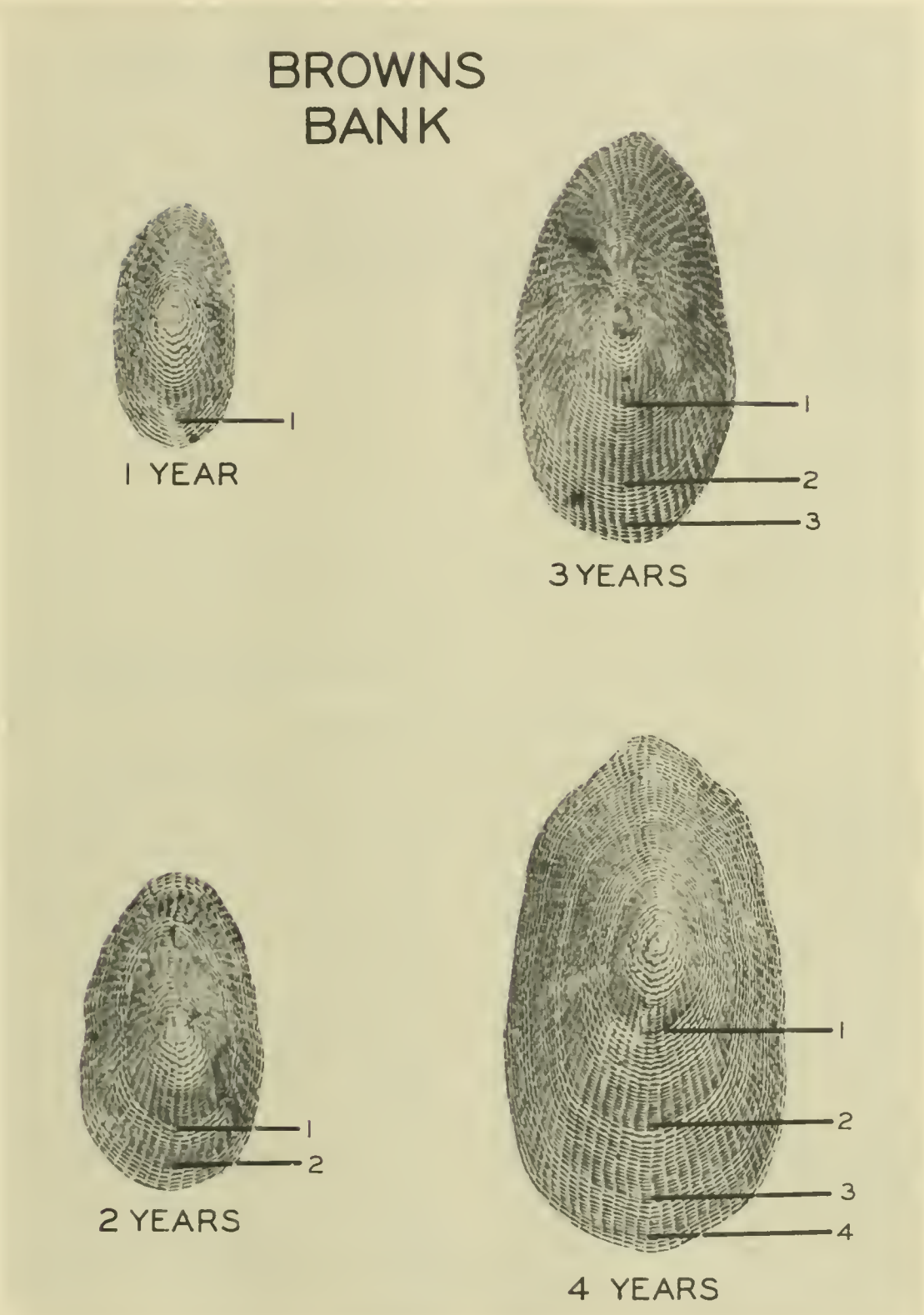

FIGURE 3b.—Impressions of scales of 1-, 2-, 3-, and 4-year-old haddock from Browns Bank.

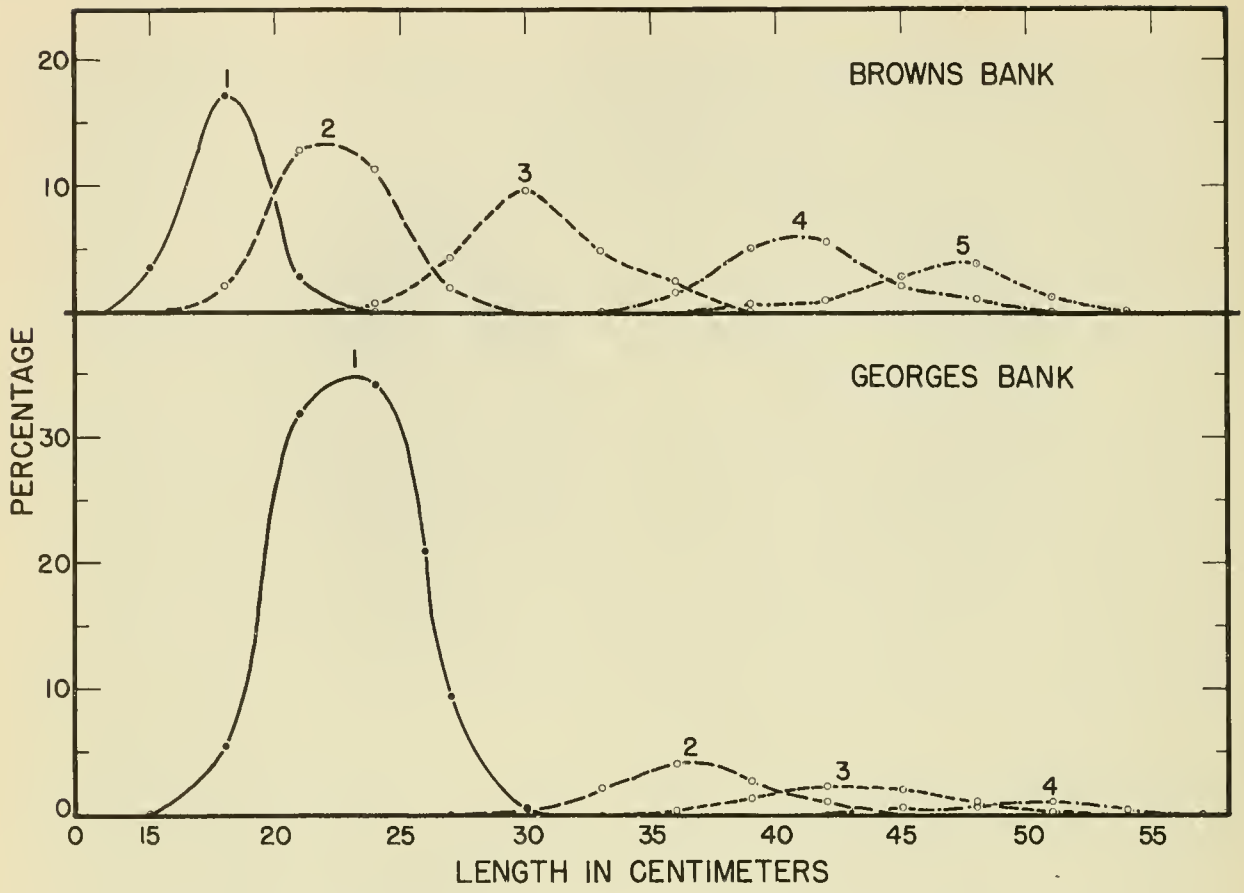

FIGURE 4.—Percentage age compositions of haddock catches from Georges and Browns Banks.

error. The variation within the age groups was such that if sampling continued, about 95 percent of the mean lengths obtained might be expected to fall within the limits indicated.

The differences in average length between the Georges and Browns Banks fish for each age were found to be highly significant.[2] The F-test (produced by the analysis of variance of the lengths in tables 2 and 3) showed values far in excess of the 1 percent level. The probability is much less than 1 in 100 that such a large difference in the average length at each age would be due to chance sampling of a homogeneous population of fish. If average lengths are plotted against age for the Browns Bank data, it is seen that the curve is not as smooth as that for the Georges Bank data and that two points (2- and 3-year-olds) seem particularly at variance with (below) what we might expect in a "normal" growth curve. We believe this is due to the fact that, in general, there is variability in growth rate between different year classes and one cannot expect to obtain a smooth or "normal" growth curve from a single year's collection of data. Specifically, we contend that the 1946 and 1947 year classes on Browns Bank were subnormal in attained size.

TABLE 6.—*Mean length and length range of various ages of haddock from Georges and Browns Banks*

[Averages computed from tables 4 and 5; standard errors from tables 2 and 3. Figures in parentheses show number of fish for which ages were read.]

Age	Georges Bank		Browns Bank	
	Mean length	Length range [1]	Mean length	Length range [1]
1 year	22.7 (105)	22.2 to 23.2	17.9 (88)	17.6 to 18.2
2 years	36.6 (352)	36.3 to 36.9	22.4 (136)	22.0 to 22.8
3 years	43.2 (251)	42.7 to 43.7	30.6 (119)	30.1 to 31.1
4 years	49.4 (92)	48.7 to 50.1	41.1 (61)	40.2 to 42.0
5 years	52.4 (14)	50.2 to 54.6	46.4 (42)	45.4 to 47.4
6 years	59.1 (6)		51.6 (7)	
7 years	(0)		52.7 (5)	
8 years	62.0 (2)		59.0 (2)	
9 years and over	72.0 (1)		63.0 (2)	

[2] Ages 1 to 5 only. No tests of significance were computed for older ages.

[1] Mean±2 times its standard error.

After this report was begun, the *Albatross III* completed its 1950 summer census on Browns Bank and there became available a means of testing this hypothesis: If true, the 3- and 4-year-olds taken in 1950, rather than the 2- and 3-year-olds in 1949, might be found to be smaller than expected. To investigate this, we computed the average size at each age of all haddock from which scales were taken on Browns Bank in 1950. These average lengths in centimeters are as follows:

	Average length	*Number included*
1-year-olds	19.3	43
2-year-olds	26.3	141
3-year-olds	31.5	122
4-year-olds	38.5	164
5-year-olds	48.0	180
6-year-olds	51.4	162
7-year-olds	55.1	117

If these values are plotted it can be seen that the points for 3- and 4-year-olds do fall below the general trend. Thus it appears that the 1946 and 1947 year classes actually had smaller attained sizes, and this appears to be a reasonable explanation for not obtaining a smooth growth curve from the 1949 collection of data on Browns Bank.

A completely chance sampling of a homogeneous population in nature is difficult to obtain, but we believe that our sampling was sufficiently representative to confirm the differences described here. First, the haddock were caught over several hundred square miles of Georges Bank and over about 100 square miles of Browns Bank. Such large areas were not covered thoroughly, of course, but the net was set at random within them. Second, the same otter-trawl net was used on the two banks and it should have sampled similarly the same-size fish on the two banks and unquestionably should have made no selection of different ages at the same size. Third, from extensive (unpublished) studies of the catch of the commercial fleet on Georges Bank we know that haddock from different parts of Georges Bank grow at rather similar rates. The other possible objection to the tests of significance concerns the "normality" of the size distributions for various ages. Inspection of figure 4 indicates that all curves are close to normal except the flat-topped one for 2-year-old haddock from Browns Bank; even this one instance of kurtosis should have little effect on the tests of significance.

SUMMARY

The haddock on Georges and Browns Banks grow at different rates. One-year-old haddock averaged 22.7 centimeters on Georges Bank as compared with 17.9 centimeters on Browns; 2-year-olds averaged 36.6 on Georges, 22.4 on Browns; 3-year-olds were 43.2 on Georges, 30.6 on Browns; 4-year-olds were 49.4, and 41.1; and 5-year-olds were 52.4, and 46.4. This difference indicates that hereditary or ecological conditions governing growth are different in the two areas and that important intermigrations of the bottom-dwelling stages of haddock do not occur. As a consequence, we need not expect the stocks to fluctuate simultaneously and we should continue to collect and to analyze separately for the two areas the statistics of landings, age, growth, abundance, and other biological data.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*

FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

A UNIQUE BACTERIUM PATHOGENIC FOR WARM-BLOODED AND COLD-BLOODED ANIMALS

By Philip J. Griffin and Stanislas F. Snieszko

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CONTENTS

	Page
Description	187
Pathogenicity	188
Discussion	189
Summary	189
Literature cited	190

A UNIQUE BACTERIUM PATHOGENIC FOR WARM-BLOODED AND COLD-BLOODED ANIMALS

By PHILIP J. GRIFFIN[1] and STANISLAS F. SNIESZKO,[2] *Bacteriologists*

The vast majority of bacterial fish diseases are caused by motile or nonmotile Gram-negative bacteria. Some of these, such as *Bacterium salmonicida*, have stable characteristics and represent bacterial species with well-defined properties. There are, however, many inadequately described motile Gram-negative bacteria which have been isolated from diseased warm- and cold-water fishes, amphibians, and reptiles from all over the world. Many of these bacteria belong to the genus *Pseudomonas*. Some bacteria, pathogenic to amphibians and reptiles (Hinshaw and McNeil 1946, 1946a, 1947), have been recently described and classified as paracolons.

The microorganism described in this report has a peculiar taxonomic position, because some of its characteristics indicate that it should be classified as a pseudomonad, while its physiological and antigenic properties suggest relationship with the paracolons.

Paracolon organisms isolated from outbreaks of gastrointestinal diseases in man have been described as a group of aberrant coliform organisms comprising a distinct biological group (Stuart et al. 1943). Borman, Stuart, and Wheeler (1944) referred coliform-like bacteria that slowly fermented lactose to a separate genus, *Paracolobactrum*. Those organisms which produced acetylmethylcarbinol were termed *Paracolobactrum aerogenoides*.

This report is believed to be the first description of organisms conforming largely to the description of *Paracolobactrum aerogenoides* and pathogenic for fish. Microorganisms were isolated from the body cavities of four aquarium fish belonging to several species (*Corydoras aeneus*, *Xiphophorus hellerii*, *Platypoecilus maculatus*, *Lebistes reticulatus*) all of which had died suddenly within a period of a week. One strain (1) was obtained from a living, infected *Corydoras aeneus*.

We are indebted to Dr. E. K. Borman, Bureau of Laboratories, Connecticut State Department of Health, Hartford, for preliminary antigenic typing and for his advice and comments, and to Dr. S. H. Hutner, Haskins Laboratories, New York, and to Dr. R. W. Hinshaw, Camp Detrick, Md., for advice and reading of the manuscript.

DESCRIPTION

In all cases observed, lesions developed on one side of the body as small areas of greenish discoloration just under the skin between the pectoral and ventral fins. Upon incision, a fetid and purulent material was exuded. A Gram stain of the discharge revealed numerous Gram-negative rods, 1.3 to 2 microns long and 0.7 micron wide, with rounded ends, and exhibiting bipolar staining.

In broth and on agar, the bacteria were arranged singly, in pairs, and occasionally in filaments. The rods were encapsulated, as determined by Anthony's method, and did not form endospores. Active motility was observed and single polar flagella were demonstrated by Novel's method (1939). The organisms were facultatively anaerobic but grew best with unrestricted access to air. In nutrient broth, the optimum growth temperature was 37° C., the maximum 43° C., and the minimum 5° C. The *p*H range for growth was from 5.0 to 9.5 with the optimum range between 6.5 and 7.5; best growth occurred at *p*H 7. Cultures maintained for almost 8 months in the refrigerator still contained viable organisms.

On nutrient agar, colonies averaged 2 mm. in diameter in 24 hours. They were circular, smooth, entire, slightly convex, and opaque. On blood agar, strains 1 and 2 exhibited a beta hemolytic zone averaging 7 mm. in diameter in 24 hours. After 48 hours the colonies were surrounded by a 16-mm. hemolytic zone with a greenish-brown

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discoloration. Strain 3 was nonhemolytic. Blood-agar and nutrient-agar cultures had a strong odor similar to that detected in the incised lesion from the infected fish. Colonies on eosin-methylene-blue and MacConkey's agars appeared glistening and colorless. On agar slants, growth was abundant, filiform, glistening, butyrous, and colorless. The appearance of the medium remained unchanged. In nutrient broth a pellicle was formed; there was dense clouding and a scant flocculent sediment. A loopful of a 48-hour broth culture inoculated into nutrient broth resulted in visible growth in 4 hours at 37° C.

At 20° C., growth in gelatin was best at the top, with subsequent stratiform liquefaction. At 37° C., liquefaction was complete in 24 hours. Nitrates were rapidly reduced to nitrites. The methyl-red test was negative. Acetylmethylcarbinol and indole were produced by strains 1 and 2. Strain 3 produced acetylmethylcarbinol but failed to form indole. Growth occurred on Simmon's citrate agar. In Koser's citrate broth, strain 1 was negative, strains 2 and 3 positive, after 3 days. Hydrolysis of cornstarch was complete in 24 hours (no color with iodine). Digestion of egg albumin and Loeffler's serum slants began in 48 hours and was practically complete in 96 hours. H_2S was not produced in Pb acetate medium or in Kligler's iron agar. The urease test was negative. There was slight acid production (*p*H 6) with the formation of a small amount of precipitate in bromocresol-purple milk. Peptonization was evident in 48 hours and practically completed in 120 hours. Litmus milk was reduced in 24 hours.

Various sugars, alcohols, and glucosides were sterilized by filtration through a porcelain filter and incorporated into standard basal medium in 1-percent concentrations. On original isolation, strains 1 and 2 produced acid in lactose after 21 days, and culture 3 after 27 days. This conforms to the behavior of the paracolon type of microorganisms which are described as slow lactose fermenters in Bergey's Manual (Breed, Murray, and Hitchens, 1948). After several serial transfers in lactose broth, the time of acid formation in lactose was reduced by 6 to 11 days, depending on the strain. Readings made during a 4-week period showed that acid and gas were produced in 24 hours at 25° C. and at 37° C. in L-arabinose (weak), glucose, D-fructose, D-mannose, sucrose, maltose, trehalose, soluble starch, dextrin, glycogen, and mannitol. A faint acid reaction and trace of gas appeared in salicin after 4 to 6 days' incubation at 37° C. At 25° C., salicin was fermented by all 3 strains in 24 hours. Strain 3 differed from strains 1 and 2 in that it produced acid and gas in raffinose but not in sucrose at either temperature. No acid or gas was produced in D-xylose, L-rhamnose, cellobiose, mellibiose, melizitose, inulin, glycerol, erythritol, adonitol, dulcitol, D-sorbitol, inositol. and esculin, at 25° C. or 37° C.

Preliminary antigenic analysis indicated that strains 1 and 2 were antigenically diverse from any of the paracolon types described by Stuart et al. (1943). Strain 1 proved to possess somatic components XXX and XL of the *Salmonella* group, while all tests with flagellar antisera were negative. Strain 2 was rough and consequently could not be typed. Strain 3 was negative for somatic components I to XXXVIII and for all flagellar antigens.

PATHOGENICITY

Nine goldfish (*Carassius auratus*) and 27 adult white mice were inoculated intraperitoneally with 0.2 ml. of 24-hour broth cultures of the 3 strains, and in 19 hours all were dead. In every instance, the organisms were reisolated in almost pure culture from the fluid present in the body cavity. Similar tests were made with 0.2-ml. suspensions of heat-killed bacteria and filtrates from the same 24-hour nutrient broth cultures. All fish and mice proved refractory. Strain 3 also proved to be pathogenic for guinea pigs.

Further experiments were carried out at the Microbiological Laboratory, Kearneysville, W. Va., in which 60 fingerling trout were used. Ten trout of each of the following species were inoculated intraperitoneally with 0.2 ml. of a 24-hour broth culture: Rainbow trout (*Salmo gairdnerii*), eastern brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*). As controls, 10 fish of each of these species were inoculated with sterile broth. The temperature of the water in the troughs was approximately 14° C. Some deaths

occurred within 24 hours after inoculation, and in less than 41 hours eight of the rainbow and all the brook trout were dead. All controls of these two species lived. Results of the brown-trout inoculations were not as striking as those of the other two species. In 48 hours six of the brown trout had died, but three of the control fish also were dead. There were no further deaths in either group.

Gross pathological changes were observed in inoculated yearling trout of the three species. Inoculations were performed, as previously indicated, using strain 1. Dead and living fish were examined. Macroscopically, the artificially infected trout did not show any external lesions other than slight swelling and congestion in the anal region. The most important and characteristic internal pathological changes noted were as follows: Intestine filled with a yellow or white gelatinous mucus, particularly in the posterior portion; blood vessels congested and intestinal wall swollen; liver redder in color than in the controls, and spleen enlarged and much darker. There was some exudate in the peritoneal cavity and occasionally the peritoneum in the posterior portion of the abdominal cavity was congested.

DISCUSSION

Biochemically, the organisms described in this paper are very similar to *Paracolobactrum aerogenoides;* but the possession of a single polar flagellum would place the bacteria in the genus *Pseudomonas.* It is interesting to note that cultures 1 and 2 differed from classical description of members of the *Paracolobactrum* group in that they formed indole and acetylmethylcarbinol. The production of both substances is not a common occurrence within this genus. Though the slow fermentation of lactose, its pathogenicity, and presence of some *Salmonella* somatic antigens suggests relationship to paracolons, the possession of a single polar flagellum would, according to the present taxonomic concepts, relate these organisms to the genus *Pseudomonas.*

Paracolon types have been described in warm-blooded and cold-blooded animals. Edwards, Cherry, and Bruner (1943) reported isolating a paracolon type from the liver of a rattlesnake. Hinshaw and McNeil (1946a) reported the isolation of paracolon types that caused heavy mortality in turkey poults. The same authors (1946b) isolated related paracolon types from the livers of rattlesnakes, suggesting a relationship between the types isolated from snakes and those causing infection in turkeys. Hinshaw and McNeil (1947) reported the isolation of two sucrose-fermenting paracolon types possessing antigenic components of the *Salmonella* group from Pacific fence lizards and of paracolons from gopher snakes and sick turkey poults.

Members of the genus *Pseudomonas* have been isolated repeatedly in outbreaks of disease of fishes and other cold-blooded animals (Schaperclaus 1941, Guthrie 1942). The relative frequency of isolations of these groups of bacteria from other cold-blooded animals, and the isolations described in this paper, call attention to the possibility that fish may be carriers of these microorganisms. It is also possible that the converse is true, that fish acquire infection from organisms carried by higher animals. The fact that these organisms have been shown experimentally to be pathogenic for both cold-blooded and warm-blooded animals places them in a unique position and leads one to speculate on the role played by fish with respect to infection in man.

SUMMARY

The isolation and description of a unique bacterium pathogenic for warm-blooded and cold-blooded animals is discussed.

The microorganism described in this report has a peculiar taxonomic position in that its single polar flagellum is a characteristic of the genus *Pseudomonas,* whereas relationship to the paracolons is suggested biochemically by its physical and antigenic properties. Paracolon organisms producing acetymethylcarbinol and classified as *Paracolobactrum aerogenoides* have been isolated from the gastrointestinal tract of man during epidemics, but this is believed to be the first description of an organism similar to *P. aerogenoides* pathogenic for fish.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

ESTIMATION OF SIZE OF ANIMAL POPULATIONS BY MARKING EXPERIMENTS

By Milner B. Schaefer

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CONTENTS

	Page
Simple case	191
The problem	191
Some applications in the literature	192
Some further considerations	195
Repeated sampling of a constant population	196
Estimation of a changing population	199
Literature cited	203

ESTIMATION OF SIZE OF ANIMAL POPULATIONS BY MARKING EXPERIMENTS

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Determination of population numbers is basic to studies of changes in populations of animals and of the causes of the changes, such as the effects of fishing on a population of fishes. For many animals this cannot be accomplished by direct enumeration, and recourse must be had to indirect methods. One technique which has been employed in the study of fishes, and other organisms as well, and which is still in course of development, is the use of marked members to estimate population numbers.

SIMPLE CASE

THE PROBLEM

The simplest case with which we have to deal, and which can be applied to many fish populations, is where we have a population containing N members (unknown) which is known to contain T marked members and $U=N-T$ unmarked, and where we have drawn a single representative sample of n members containing t marked and $u=n-t$ unmarked. The term "representative" is used here to mean that the character estimated from the sample will have a mean value in repeated samples equal to the population value. This corresponds with the commonly accepted sense of the term, and also with its usage by Neyman (1934). A simple random sample of the population is representative, but so also may be various others.

The problem of estimating N consists in making such an estimate given T and the sample values n, t, and u. The usual basis of procedure is to accept $\frac{N}{T}=\frac{n}{t}$ intuitively and to estimate N by the equation

$$N=\frac{nT}{t} \quad \ldots\ldots\ldots\ldots \quad (1)$$

If, for example, we know there are 100 marked members in the population, and a sample of 500 contains 50 marked members, we would estimate the population by this equation to be

$$N=\frac{500\times 100}{50}=1{,}000$$

This method has been employed by a considerable number of investigators during the last two decades to estimate the populations of various organisms. The method is much older than this, however, having been employed as early as 1783 by the famous French mathematician and scientist Laplace in estimating the human population of France. Laplace gave considerable attention to the theoretical problem of the error involved in employing this method. This problem attracted the attention of another famous statistician, Karl Pearson, who published an analysis of it in 1928. Later workers in various branches of zoology seem to have overlooked Pearson's work and also that of their zoological contemporaries. They have apparently often "rediscovered" the same method, but have in the main given little or no attention to the problem of the accuracy of the resulting estimate.

Laplace determined from a sample the ratio of births in a year to the population producing those births, and then ascertained the number of births in a year in each urban and rural district of France; by multiplying the number of births by the ratio of population to births determined from the sample, he arrived at an estimate of the total population. Laplace was led to consider also the error inherent in his estimate. This problem, as restated by Pearson (1928), but using my notation, is as follows: "A population of unknown size N is known to contain T affected or marked members. It is desired to ascertain—on the hypothesis of inverse probabilities—a measure of the error introduced by estimating N to be $n\frac{T}{t}$, where t is

955629° — 51

the number of marked individuals in a sample of size n." Laplace treated this problem as an urn problem, with an infinite number of black and white balls representing marked and unmarked members. On the basis of an extension of Bayes' theorem, he predicted from a first sample of t and n observed what a second sample with known T but unknown N might produce. He found that the mean value of N would be equal to $\frac{Tn}{t}$ if T, n, and t are all large. He also took the distribution of N to be normal about $\frac{Tn}{t}$ as mean with standard deviation estimated by

$$\sigma_N{}^2=\frac{Tu(T+t)(t+u)}{t^3} \quad \ldots\ldots \quad (2)$$

where the numbers are all large.

For the preceding example, where $T=100$, $n=500$, and $t=50$, Laplace's solution would give an estimate of standard deviation

$$\sigma_N=\left(\frac{100\times450\times150\times500}{50^3}\right)^{\frac{1}{2}}=164$$

Pearson reexamined this problem in his 1928 paper because he felt Laplace's urn statement did not fit the actual problem since "We are not taking a second sample from an infinite population. We have only one sample and we want to learn something about the population from which it has been sampled, which is finite in extent, although its extent is unknown. We do know, however, that it contains T white balls; i. e., births in all France."

Assuming the sample n to be a random sample of the finite population N, and on the basis of inverse probabilities (Bayes' theorem), Pearson finds that the modal value of the distribution of the possible values of N is

$$\tilde{N}=u+T+\frac{u(T-t)}{t}=\frac{nT}{t} \quad \ldots\ldots \quad (3)$$

the mean value is

$$\overline{N}=u+T+\frac{(u+1)(T-t+1)}{(t-2)} \quad \ldots\ldots \quad (4)$$

and the variance is

$$\sigma_N{}^2=\frac{(u+1)(T-t+1)(n-1)(T-1)}{(t-2)^2(t-3)} \quad \ldots \quad (5)$$

where t, u, and T are all large. Laplace's case,

$$\overline{N}=\tilde{N}=\frac{nt}{t} \quad \ldots\ldots\ldots \quad (6)$$

and

$$\sigma_N{}^2=\frac{Tu(T-t)(t+u)}{t^3} \quad \ldots\ldots \quad (7)$$

This estimate of $\sigma_N{}^2$ is different from and smaller than that of Laplace, the disagreement being attributed by Pearson to Laplace's taking his sampled population as if it were a second sample independent of that already taken.

For the example employed before, with $T=100$, $n=500$, $t=50$, formula 7 would give

$$\sigma_N=\left(\frac{100\times450\times50\times500}{50^3}\right)^{\frac{1}{2}}=95$$

Pearson's paper seems to have been generally overlooked by zoologists dealing with similar problems.

SOME APPLICATIONS IN THE LITERATURE

Formula 1 has been applied to the estimation of diverse animal populations. One of the best known of these applications is the so-called Lincoln index of the duck population of North America developed by Lincoln (1930), and mentioned in the textbook of Leopold (1935), the monograph of Kendeigh (1944), the manual of Wright (1939), and elsewhere. Lincoln used the ducks banded at stations in North America as his marked members, and the kill by hunters as his sample of the population. The inaccuracies of kill records and the incomplete return of bands were recognized as sources of errors. No attempt was made to estimate the statistical error.

An application of this method was made by Vorhies and Taylor (1933). These workers computed the number of jack rabbits on fenced cattle ranges of Arizona by taking the ratio of jack rabbits seen to the number of cattle seen in a strip of width equal to the apparent flushing distance of the jack rabbits, and comparing this ratio with the known number of cattle on the range. In this case, the cattle would represent the "marked" members of the population of rabbits plus cattle. It seems rather doubtful whether the ratio in the sample would be a fair estimate of the ratio in the population because of the obviously different

visibility of cows and rabbits, even in a narrow strip.

Jackson (1933) developed a method of computing the population of tsetse flies in a closed area by marking flies with colored paint and taking a sample to determine the ratio of marked to unmarked. In a later paper (1936) Jackson states that he discovered this method independently in 1930, but meanwhile became cognizant of Lincoln's work and hastens to credit Lincoln with the method.

Jackson mentioned, also, that a representative sample of the population as regards mark ratios would be obtained if either the marking or the subsequent sampling were carried out in a nonselective fashion. This is of considerable practical importance. It is not necessary that both be nonselective. If the marks are randomly, or evenly, distributed in the population, any sample of n members will yield a consistent estimate of the mark ratio in the population. (The term "mark ratio" or "tag ratio" will be used in this paper to mean the quotient of the number of marked members in a group divided by the total members in the group.) Similarly, a representative sample of the population will yield a consistent estimate of the mark ratio regardless of the distribution of marked members in the population.

Sato (1938) estimated the stock of red salmon in the western North Pacific. He stated:

> 2. The stock (S) of red salmon may be estimated by the formula:
>
> $$Y:X=S:Z,$$
>
> where Y is the number of tagged fishes, X, the number of recaptured fishes, and Z, the total catch of the fish.

His estimate of 94.7×10^6 individuals in 1936 was made from 1,358 marked fish and 177 recaptures among a sample of $12{,}339\times10^3$. He made no attempt to estimate the reliability of the result. It may be seen from formula 7, however, that the sampling error is actually quite large.

Green and Evans (1940) employed this method for computing populations of snowshoe hares. Hares were trapped and banded during a long "precensus period" lasting all winter and up to mid-April. The banded hares at liberty from these operations were taken as the known number of marked members, and the ratio of marked to unmarked was determined during a short "census period" in April. The formula employed by these authors is essentially formula 1, since they take

$$\frac{\text{Hares banded in precensus period}}{\text{Other hares present in precensus period}} = \frac{\text{New-banded hares trapped in census period}}{\text{Other hares trapped in census period}} \quad . \; . \; (8)$$

and compute the number of "other (unmarked) hares present in precensus period," and add it to the number of marked hares to get the total population. This may be illustrated by the simple example we have employed before, where we have a population containing 100 marked members and draw a sample of 500 containing 50 marked members. Green and Evans would compute "other hares present in precensus period," as follows:

$$\frac{100}{X}=\frac{50}{450} \qquad X=900$$

and add the 100 marked hares to get the population estimate of 1,000.

These authors consider the effects of several possible sources of error. They show that migration in and out of the area of study is unimportant. The "evenness" of the sampling is also considered. They state that "It is essential that trapping throughout the area be uniform during the census retrap in the spring. . . . Uniformity need not be so rigidly maintained during the precensus period." This, of course, is a special case of the rule that either the sampling for tagging must be uniform or the subsequent sampling for tag ratio must be such as to yield a representative sample of the whole population.

Green and Evans also consider the "error of random sampling." Using their notation, we find that they take:

p = proportion of hares trapped in census period that were not banded (trapped) in precensus period.
P = number of the hares trapped in census period that were not trapped (banded) in precensus period.
N = total number of hares trapped in the census period.

$$p=\frac{P}{N}$$

They then take σ_p for the standard deviation of p and state that

$$\sigma_p=\sqrt{\frac{pq}{N}} \quad . \; . \; . \; . \; . \; . \; . \; . \; (9)$$

where $q=1-p$. Taking $P\pm2\sigma_pN$, and employing these values in place of the second quotient

in their formula (8), they arrive at an estimate of range of the error due to sampling. They conclude that—

> If we use $2\sigma_p$ as our range on either side of the figure obtained . . . we are almost certain to include the correct figure for p, since twice the standard deviation on either side of the mean includes 95 percent of a normal distribution curve.

While this estimate of the reliability of the population estimate is better than none and, indeed, will give an idea of limits within which the population may be expected to fall, it suffers from a lack of precision. The method of computation may be illustrated by the simple numerical example we have employed before. Here $P=450$, $N=500$, and $p=0.90$. Formula 9 then yields

$$\sigma_p=\sqrt{\frac{.9\times.1}{500}}=.01342$$

and $2\sigma_p N=13.42$. The corresponding values of 463.4 and 436.6 may be employed in the second quotient of formula 8 in place of 450 for P to obtain estimates of 927 and 873 for limits of the estimate of "other hares present in precensus period." Corresponding values of total population are 1,027 and 973.

Formula 9 gives the standard deviation of p in repeated samples of size N from a population of infinite size. Since in the present case the population is finite, and N is large with respect to it, the formula for the standard deviation of p should be

$$\sigma_p{}^2=\frac{P-N}{P-1}\frac{p\cdot q}{N}$$

where P=the number in the population (Cramer 1946, p. 516; Kendall 1944, p. 203). Thus Green and Evans' limits for p would tend to be too broad. For the same simple example used above, this formula gives us

$$\sigma_p{}^2=\frac{(1000-500)}{(1000-1)}\frac{0.9\times0.1}{500}=.0000901$$

$$\sigma_p=.00949$$

Green and Evans' estimate also has, however, the same objection that Pearson raised to Laplace's solution, rather important in this instance, that this treats the problem of a further sample from a population in which the value of p is known, which is not the same thing as determining the error of the estimate of the population from the single sample available.

Dice (1941) refers to the paper by Green and Evans and considers a number of practical factors to be taken into account in carrying out the sampling.

Knut Dahl (1943, pp. 139–143), has applied the method of marked members to enumeration of trout in a lake. In a small lake on the west coast of Norway, of 250,000 square meters, trout were captured by beach seine and marked. During a second fishing 8 to 14 days later he determined the number of marked and unmarked fish captured. From the number of marked fish liberated, divided by the number of marked fish recaptured, he computed a "Gjenfangstkvotient" by which the total fish taken in the second fishing was multiplied to obtain the total population. This is, of course, the same as formula 1, where $\frac{T}{t}$ is the "Gjenfangstkvotient."

Ricker (1942) mentions the simple case here considered, although he uses a method of repeated tagging and sampling on the stationary populations of pond fishes dealt with in his paper. This method will be reviewed subsequently.

In a later paper, Ricker (1945a) employs formula 1, which he calls "the Peterson method," after the Danish investigator who is said to have used it on plaice. Ricker's field procedure is similar to that of Green and Evans on hares in that he used the number of fish marked during a precensus period and the mark ratio of a later period. He also writes in regard to the sampling consideration we have discussed earlier in relation to Jackson (1936) that:

> The principle involved here is that if either the marking *or* the search for recaptured fish is made on only a part of a homogeneous population, the Peterson estimate will still apply to the whole population. If both marking and search are made in only a fraction of the population, the estimate applies to whichever fraction is larger.

Cagle (1946) employed marked lizards to estimate their population on a section of Tinian Island by the employment of the method formulated in formula 1. He marked 127 individuals by clipping their toes and in a sample of 52 found 12 marked, yielding an estimated population of roughly 500 individuals. He did not consider the problem of sampling error.

SOME FURTHER CONSIDERATIONS

An alternative derivation

Formulae 3 to 7 were reached by Pearson by means of Bayes' theorem, which is objected to as invalid by many mathematical statisticians (Kendall 1944, p. 176 et seq.). Dr. S. Lee Crump has suggested (private communication) that an estimate of N may be arrived at by other means, as follows. Drawing samples of fixed size n from a population N of which T are marked, the probability that, in a sample of n, t are marked is

$$P(t)=\frac{(N-n)!n!T!(N-T)!}{N!t!(T-t)!(n-t)!(N-T-n+t)!} \quad \ldots (10)$$

whence

$$E\left\{\frac{(n+1)(T+1)}{(t+1)}\right\}=N+1-P(O)(N-T-n) \ldots (11)$$

where $E(\ )$ denotes mathematical expectation and $P(O)$ is the probability of getting no tags in the sample.

This means that

$$\frac{(n+1)(T+1)}{(t+1)}-1 \quad \ldots \ldots \quad (12)$$

is an estimate of N biased by an amount $P(O)(N-T-n)$. If conditions are such that a sample of n with no marked individuals is very unlikely, the bias is negligible. We may say that formula 12 is an effectively unbiased estimate of N.

Where the numbers are all large, formula 12 reduces immediately to formula 1 or formula 6.

Unfortunately, an estimate of the variance of the estimate of N given in formula 12 has not yet been obtained.

Chapman (1948) has considered the problem of determining the value or values of N which make $P(t)$, formula 10, a maximum. He found that the maximum-likelihood estimate of N is $\frac{nT}{t}$, or if that is fractional, the integer immediately below $\frac{nT}{t}$.

Confidence limits on the population estimate

The method of confidence intervals, due to Neyman (1934), may be employed to determine the range of values within which we may expect N to lie. A discussion of the theory of confidence intervals is beyond the scope of this paper, and reference is made to the original paper of Neyman or to the discussion of Cramer (1946, p. 507 et seq.) or that of Kendall (1946, p. 62 et seq.).

The confidence limits of the estimate of the tag ratio in the population may be obtained as follows (Cramer 1946, p. 515):

> Suppose we have a population consisting of a finite number N of individuals, Np of which possess a certain attribute A, while the remaining $Nq=N-Np$ do not possess A. It is now required to estimate the unknown proportion p . . . Let us draw a random sample of n individuals *without replacement*, and observe the number v of individuals in the sample possessing the attribute A. In current text-books on probability, it is shown that we have
>
> $$E\left(\frac{v}{n}\right)=p \qquad D^2\left(\frac{v}{n}\right)=\frac{N-n}{N-1}\cdot\frac{pq}{n}$$
>
> Further the variable $p^*=\frac{v}{n}$ is approximately normally distributed, when n and $N-n$ are large. Taking p^* as an estimate of p, we now assume as above that the error of approximation in the normal distribution can be neglected. The probability that p^* lies between the limits $p\pm\lambda\sqrt{\frac{N-n}{N-1}\frac{pq}{n}}$ is then equal to ϵ, where λ has the same significance as in the preceding example. (Note: where λ was stated to be the $100\epsilon\%$ value of a normal deviate, and ϵ is the confidence level.)

In Cramer's notation $E(\ )$ denotes mathematical expectation (or mean value) and $D^2(\ )$ denotes the variance.

N and n have the same meaning as in our earlier formulae, 1 to 12; p is equal to $\frac{T}{n}$, and v is equal to t in those formulae.

For any given values of N, n, and T we can calculate the limits within which $p^*=\frac{t}{n}$ may be expected to fall for a given confidence level, ϵ, by the formula

$$p\pm\lambda\sqrt{\frac{N-n}{N-1}\cdot\frac{pq}{n}} \quad \ldots \ldots \quad (13)$$

where

$$p=\frac{T}{N} \text{ and } q=1-p$$

Given values of n and T from an experiment, we can, then, by formula 13 calculate for various values of p, as ordinates, the limits within which p^*, the tag ratio of the sample, as abscissae, may be expected to fall for a given value of the confidence level ϵ. The curves connecting these points will form the confidence limits corresponding

to various values of sample tag ratio $p^*=\frac{t}{n}$. Since to every value of p there corresponds a value of N, these curves also give the confidence limits of our estimate of the size of the population made by the formula

$$N=\frac{T}{p^*} \quad \ldots\ldots\ldots \quad (14)$$

which is the same as formula 1, of course.

A numerical example may make this clear. Suppose that in a given experiment we have placed 1,000 tagged fish in the population and plan to draw a sample of 2,000 fish for determining the tag ratio. By formula 13 we can compute for values of population tag ratio, p, the limits within which p^* will be expected to fall in, say, 95 percent of the cases ($\epsilon=0.95$). In figure 1, we have calculated and plotted these limits for part of the range of p for this example. The ordinates on this graph are values of p, and the abscissae are values of p^*. Going horizontally across the graph for a given value of p we come to the values of p^* within which samples of 2,000 from a population having a true tag ratio of p would be expected to fall in 95 percent of the cases. By the theory developed by Neyman the loci of such points for various values of p form the 95-percent confidence limits for values of p^*. For a given value of p^* we go along the vertical to the intersections with these loci to find the confidence limits for that value of p^*. Thus, suppose that we draw our sample of 2,000 and find that it contains 100 tagged fish. Our estimate of the tag ratio in the population is 0.05, and from figure 1 we find that for this value of p^* the 95-percent confidence limits are 0.042 and 0.059. Since we know there are 1,000 tagged fish in the population, our estimate of the population by formula 14 is 20,000 with 95-percent confidence limits 16,950 and 24,800. On the right-hand edge of the graph we have plotted the values of N corresponding to tag-ratio values of the same ordinates on the left-hand edge, in order to exhibit graphically the relation between the two.

Such a chart as this may be computed for any particular experiment. The entire range of values of p need not be included; it is sufficient in practice to compute the values to include the region within which p^* is expected to fall.

For values of n which are small with respect to N, so that $\frac{N-n}{N-1}$ approaches 1, formula 13 approaches the form appropriate for the binomial. Clopper and Pearson (1934) have computed and charted the confidence limits of the binomial for a large number of values of n for 95 percent and 99 percent confidence levels. Since the limits for the binomial fall in every case outside the limits given by formula 13, these charts may be used to obtain upper and lower limits on the sample value of p^* even where n is not small in relation to N. This involves, of course, a considerable loss of efficiency when n is not small in relation to N, so that the employment of formula 13 would seem to be generally preferable in such cases.

Chapman (1948) has considered the Poisson approximation to the distribution of expected numbers of tag recoveries where the tag ratio is low, in addition to the normal, normal-binomial, and normal-hypergeometric approximations, as bases for confidence-interval estimates of N. He has tabulated useful confidence limits for the Poisson distribution, and discusses practical criteria for judging which distribution to choose as a basis of estimation for various values of n and $\frac{t}{n}$.

As is shown by Chapman's example on page 81 of his paper, for experiments involving numbers of tagged fish, T, and subsequent samples, n, of the magnitude of the example we have employed, and which is of the approximate magnitude of most practical tagging experiments, the differences in confidence limits resulting from the several distributions which might be employed are not very great. In practice it would make little difference which we chose. He recommends which distribution to employ for various situations; for values of $n>1{,}000$ and $\frac{t}{n}>0.05$ he recommends the normal hypergeometric, which has been employed by me in the example above.

REPEATED SAMPLING OF A CONSTANT POPULATION

Where the population of an area remains constant over an appreciable period of time, it is possible to arrive at an estimate based on repeated sampling and marking.

In order to estimate the population by this method, a sampling station or group of stations is established that will result in a random sample of all parts of the population. Samples are drawn at intervals and the fish are tagged and replaced. Records are kept, for each sample, of the number of fish caught and the number of recaptures. Schnabel (1938) provided a solution to the problem of estimating the population from the resulting data.

We may let N be the total population, as before, T_i be the number of tagged fish in the lake when the i^{th} sample is drawn, n_i be the total number in the i^{th} sample, consisting of t_i tagged fish recaptured and u_i untagged. Schnabel finds that where k samples are drawn, the method of maximum likelihood gives as an estimate of N the positive real root of the k^{th} order equations

$$\sum_{i=1}^{k} \frac{u_i T_i}{N-T_i} = \sum_{i=1}^{k} t_i \quad \ldots\ldots\ldots (15)$$

which can be expanded in the form

$$\sum_{i=1}^{k} \frac{u_i T_i}{N} \left(1+\frac{T_i}{N}+\frac{T_i^2}{N^2}+\ldots\right) = \sum_{i=1}^{k} t_i \quad \ldots (16)$$

By taking sufficient terms in formula 16 the root may be approximated as closely as desired. Schnabel states that 3 terms of the series are usually sufficient, and that the computations necessary for higher approximations are often prohibitive.

Schnabel also considers some special cases of formula 16. By writing the equation (15) in the form

$$\sum_{i=1}^{k} \frac{n_i T_i - t_i N}{N-T_i} = 0 \quad \ldots\ldots\ldots (17)$$

it may be seen that if T_i is negligible compared to N, the root of formula 15 is approximately

$$\frac{\sum_{i=1}^{k} n_i T_i}{\sum_{i=1}^{k} t_i} \quad \ldots\ldots\ldots\ldots (18)$$

This is the formula which has been employed by fisheries workers in practice. Its application will be clear from the example given in table 1, the data for which are from a marking experiment by Krumholz (1944).

TABLE 1.—*Schnabel's method of computing a fish population by repeated sampling and marking*

[Data from Krumholz (1944) table I]

Date (1941)	Number of fish examined	Number of marked fish in lake	Product	Sum of products	Number of returns	Sum of returns	Estimated population
	n_i	T_i	$n_i T_i$	$\Sigma n_i T_i$	t_i	Σt_i	$\Sigma n_i T_i / \Sigma t_i$
July 30	53						
31	55	53	2,915	2,915	2	2	1,458
Aug. 1	67	106	7,102	10,017	3	5	2,003
2	59	170	10,030	20,047	2	7	2,864
4	85	225	19,125	39,172	6	13	3,013
5	94	297	27,918	67,090	3	16	4,193
6	53	376	19,928	87,018	1	17	5,119
7	115	426	48,990	136,008	5	22	6,182
8	59	520	30,680	166,688	4	26	6,411
9	53	573	30,371	197,059	4	30	6,569
11	53	609	32,277	229,336	5	35	6,552
12	68	604	41,074	270,410	2	37	7,308
13	45	666	29,970	300,380	4	41	7,326
14	38	705	26,790	327,170		41	7,980
15	45	742	33,390	360,560	3	44	8,195
16	28	742	20,776	381,336		44	8,667
18	40	741	29,640	410,976	2	46	8,934
19	20	741	14,820	425,796		46	9,256
20	30	741	22,230	448,026	5	51	8,785
21	27	741	20,007	468,033	1	52	9,001
22	42	741	31,122	499,155	1	53	9,418
23	20	741	14,820	513,975		53	9,698

Next Schnabel points out that if $T_i = T$ for all i

$$N = T\frac{\Sigma n_i}{\Sigma t_i} \quad \ldots\ldots\ldots (19)$$

and states that "This formula is applicable to the data of experiments in which the number tagged is held constant after a certain point. This method has the disadvantage that the data taken before T become constant are not utilized."

It may be readily seen that if we consider the sum of the samples in this last case as a single large sample, formula 19 is identical with formula 1. Thus the simple case considered earlier may be regarded as a special case of the method of the present section.

Schnabel's formula 18 has been employed by Ricker (1942, 1945a) to estimate fish populations of lakes and ponds in Indiana. Ricker has assumed that, in situations where this formula is applicable, the fiducial limits of the Poisson distribution applied to Σt_i would give some idea of the variability ascribable to random sampling (Ricker 1945b), but also states that "an estimate of error obtained directly from the data themselves, for both the general and the special case, is to be desired."

Underhill (1941) applied this method and formula 18 to the computation of a chub-sucker population of a pond in New York, and Roach

(1943) has done the same in estimating the white-bass population of an Ohio lake.

Schumacher and Eschmeyer (1943) have devised an estimate of N from repeated samplings which is different from that of Schnabel. They assume that the weight, or value, of each sample is proportional to the number of fish in the sample. Under this assumption, an estimate of N is arrived at by minimizing the sum of the squares of the weighted discrepancies of the $\frac{T_i}{N}$ from their estimates $\frac{t_i}{n_i}$. This leads to the formula

$$N=\frac{\sum_{i=1}^{k}T_i^2 n_i}{\sum_{i=1}^{k}T_i t_i} \quad \ldots\ldots\ldots \quad (20)$$

which is applied by these authors to the estimation of fish populations of a pond in Tennessee.

These authors have also derived an expression for the sampling error of N. They take as the standard error of N the square root of

$$\frac{N^3 s^2}{\sum_{i=1}^{k}T_i t_i} \quad \ldots\ldots\ldots \quad (21)$$

where

$$s^2=\frac{1}{K-1}\left[\sum_{i=1}^{k}\frac{t_i^2}{n_i}-\frac{1}{N}\sum_{i=1}^{k}T_i t_i\right]$$

In the last formula I have corrected a typographical error which appears in the original paper (formula 3, page 234) and which Professor Schumacher has kindly pointed out in a private communication.

In table 2 is recapitulated a numerical example from Schumacher and Eschmeyer (1943), pertaining to the estimation of a population of bullheads in Yellow Creek Pond, Tennessee. Substituting the appropriate sums from this table in formulae [20] and [21], we obtain the following estimates for N and its standard error (σ_N):

$$N=\frac{49{,}598{,}907}{35{,}121}=1{,}412$$

$$s^2=\frac{1}{14}\left(27.992263-\frac{35{,}121}{1412}\right)=0.2228$$

$$\sigma_N=\sqrt{\frac{(1{,}412)^3(0.2228)}{35{,}121}}=134$$

TABLE 2.—*Schumacher and Eschmeyer's method of computing a fish population by repeated sampling and marking*

[Data from table 2 of Schumacher and Eschmeyer (1943)]

Date (1941)	Number of marked fish in pond	Number of fish in sample	Number of marked fish in sample	$T_i^2 n_i$	$T_i t_i$	$\frac{t_i^2}{n_i}$
	T_i	n_i	t_i			
Oct. 3	23	39	4	20,631	92	0.410256
Oct. 6	57	49	4	159,201	228	.326531
Oct. 7	102	51	4	530,604	408	.313725
Oct. 8	149	28	5	621,628	745	.892857
Oct. 9	172	79	19	2,337,136	3,268	4.569520
Oct. 10	232	43	8	2,314,432	1,856	1.488372
Oct. 11	267	49	7	3,493,161	1,869	1.000000
Oct. 12	309	22	2	2,100,582	618	.181818
Oct. 13	329	38	11	4,113,158	3,619	3.184211
Oct. 14	356	22	5	2,788,102	1,780	1.136364
Oct. 15	372	15	4	2,075,760	1,488	1.066667
Oct. 16	383	4	1	586,756	383	.250000
Oct. 17	383	25	7	3,667,225	2,681	1.960000
Oct. 18	383	98	30	14,375,522	11,490	9.183673
Oct. 19	383	71	12	10,414,919	4,596	2.028169
Total				49,598,907	35,121	27.992263

Ricker (1945b) has investigated the relative efficiency of Schumacher's estimate (20) and Schnabel's formula (18). He states:

> From an exchange of letters with Dr. Schumacher it appears that the efficiency of this expression is at a maximum when $\frac{T}{N}$ is equal to 0.5, whereas Schnabel's second, or approximate formula becomes most efficient as $(T/N) \rightarrow 0$, and the two formulae are of equal efficiency when $T/N=0.25$. Consequently Schnabel's form will ordinarily be best, since the value of T/N rises gradually from a very small initial magnitude, and, except on quite small bodies of water, will not often exceed 0.25 even when the experiment comes to an end. Of course Schnabel's long formula, carried to several terms, can always be used if the best possible estimate is desired; but the labor of computation will rarely be warranted, considering the magnitude of the sampling and probably systematic errors in such experiments.

Krumholz (1944) has made a practical check of the accuracy of estimation of a fish population by repeated sampling, marking by clipped fins, and the application of Schnabel's formula (18). He computed the population of fish over 45 millimeters in length in the north basin of Twin Lake, Mich., in this manner and then poisoned the area with rotenone and counted the fish poulation directly. He concluded:

> The estimate from netting operations was very close to that obtained by poisoning in this first check on the fin-clipping method for estimating fish populations. Further studies of this type are needed to prove definitely the accuracy of the method. . . . Other checks of this method will be made when conditions permit.

ESTIMATION OF A CHANGING POPULATION

Some fishes, such as salmon spawning in a given stream or lake, do not always form a single, homogeneous, completely mixed population. There may be a tendency for the fish which migrate to the spawning grounds earliest to complete their spawning and die earliest; there results a positive correlation between time of migration past a point below the spawning grounds and the time of appearance on, and of death at, the spawning grounds. If, now, we are tagging fish below the spawning grounds, or even on these grounds, and later sampling for tag ratios, the "mixing" of the fish between tagging and sampling is not complete, and this may need to be taken into consideration in our estimation of the population. Similar situations may occur among other migratory animals.

When there exists such a correlation between time of tagging and time of subsequent sampling, the samples drawn during any particular part of the season do not represent all parts of the population equally; the sample is not a random sample of the whole population. The possible effects of this on our estimates by formula 1 are easily seen. If, as has already been pointed out, all parts of the population have the same tag ratio, if the tags are "evenly distributed," it will make no difference whether the subsequent samples represent the various parts of the population equally or not. Likewise, if the population is "evenly" sampled after tagging, that is, if the probability of a given fish being included in the sample is not a function of the time of sampling (and, therefore, not a function of the time of tagging), any uneven distribution of tags by time of migration will have no effect. If, on the other hand, the probability of a fish being tagged (the tag ratio) varies with the time of tagging, and the probability of being included in the subsequent sample varies with the time of sampling, and there also exists a correlation between time of tagging and time of sampling, it is obvious that the tag ratio in the total sample for the season will differ from that of the population to some extent, depending on the magnitudes of these factors.

Presented here is a method of estimating the population by which these errors may be reduced when the tagging is done by means of numbered tags, so that the relation between time of tagging and time of recovery may be estimated. I am indebted to Dr. S. Lee Crump of the Iowa State College Statistical Laboratory for much assistance with the mathematics involved.

If our tagged fish have been marked by numbered tags, we know both the date of tagging and date of recovery for each one recovered. This makes it possible to tabulate the recoveries by time of tagging and time of recovery, using as a time interval a convenient period of days. Our notations for the elements involved in the discussion of this section, in addition to those introduced before, are as follows:

Let

N_α=the total number of fish passing the point of tagging during the α^{th} period of tagging. ($\alpha=1, 2, 3, \ldots a$).

T_α=the number of these fish which are tagged during the α^{th} tagging period.

$n_{\alpha i}$=the number of fish out of the $N\alpha$ that are subsequently recovered during the i^{th} recovery period.

$T_{\alpha i}$=the number of fish out of the T_α that die and are thus available to be recovered during the i^{th} recovery period.

$m_{\alpha i}$=the number of tagged fish tagged during the α^{th} period of tagging and recovered during the i^{th} period of recovery ($i=1, 2, 3, \ldots s$).

$m'_{\alpha i}$=the number of untagged fish passing the point of tagging during the α^{th} tagging period and recovered during the i^{th} recovery period.

The following summation conventions are employed:

$$\sum_i m_{\alpha i}=m_{\alpha\cdot} \qquad \sum_\alpha m_{\alpha i}=m_{\cdot i} \qquad \sum_\alpha\sum_i m_{\alpha i}=m_{\cdot\cdot}$$

$$\sum_i m'_{\alpha i}=m'_{\alpha\cdot} \qquad \sum_\alpha m'_{\alpha i}=m'_{\cdot i}$$

$$\sum n_{\alpha i}=n_{\alpha\cdot}$$

Obviously,

$$m_{\alpha\cdot}+m'_{\alpha\cdot}=n_{\alpha\cdot}$$

Also let:

$$m_{\cdot i}+m'_{\cdot i}=C_i$$

N_i=the number of fish dying on the spawning grounds during the i^{th} recovery period.

$$q\alpha=\frac{\sum_i n_{\alpha i}}{N_\alpha}$$

$$Pi=\frac{\sum_\alpha T_{\alpha i}}{N_i}$$

The data available from a given experiment can be laid out in a table as follows:

	Period of tagging (α)			Total tagged fish recovered	Total fish recovered
	1	2	3 . . . a		
Period of recovery (i):					
1	m_{11}	m_{21}	m_{31} . . . m_{a1}	$m_{\cdot 1}$	C_1
2	m_{12}	m_{22}	m_{32} . . . m_{a2}	$m_{\cdot 2}$	C_2
3	m_{13}	m_{23}	m_{33} . . . m_{a3}	$m_{\cdot 3}$	C_3
. . .	. . .	. . .	. . . . .	. . .	. . .
. . .	. . .	. . .	. . . . .	. . .	. . .
. . .	. . .	. . .	. . . . .	. . .	. . .
S	m_{1s}	m_{2s}	m_{3s} . . . m_{as}	$m_{\cdot s}$	C_s
Total tagged fish recovered	$m_{1\cdot}$	$m_{2\cdot}$	m_3 . . . m_a	$m_{\cdot\cdot}$ (=t)	
Total fish tagged	T_1	T_2	T_3 . . . T_a		

Of course, $\sum_\alpha T_\alpha=T$ and $\sum_i C_i=n$.

Now, the number of fish passing the tagging point during α which die during period i might be estimated by

$$n^*_{\alpha i}=\frac{m_{\alpha i}}{P_{\alpha i}} \quad \ldots\ldots\ldots \quad (22)$$

(I shall denote "estimate of" by the asterisk herein) where $P_{\alpha i}$ is the probability of a fish being tagged during α and recovered during i. This probability is unknown, and our best available estimate of it seems to be the joint probability $P_i q_\alpha$, where these terms are as defined above. This amounts to taking as the probability of recovery the average probability of recovery of all the fish passing the tagging point during α, and as the probability of being tagged the average probability of being tagged of all the fish dying during period i.

If the samples drawn for tagging and the samples later drawn for tag ratios are representative of the parts of the population from which they are drawn, Pi and q_α may be estimated from the data as follows:

$$q^*_\alpha=\frac{m_{\alpha\cdot}}{T_\alpha}$$

$$\ldots\ldots\ldots \quad (23)$$

$$Pi^*=\frac{m_{\cdot i}}{C_i}$$

The estimate of $n_{\alpha i}$ is, then, given by

$$n^*_{\alpha i}=\frac{m_{\alpha i}}{q^*_\alpha P^*_i}$$

which is equivalent to

$$n^*_{\alpha i}=m_{\alpha i}\frac{T_\alpha}{m_{\alpha\cdot}}\frac{C_i}{m_{\cdot i}} \quad \ldots\ldots \quad (24)$$

The estimate of the total population is obtained by summing all these $n^*_{\alpha i}$, thus

$$N^*=\sum_\alpha\sum_i m_{\alpha i}\frac{T_\alpha C_i}{m_{\alpha\cdot}m_{\cdot i}} \quad \ldots\ldots \quad (25)$$

A somewhat more rigorous derivation, based on Bayes' theorem, has been suggested by Dr. Crump:

The problem is to estimate the $n_{\alpha\cdot}$ and the q_α. if we can do this we can take as our estimate of N,

$$N^*=\sum_\alpha\frac{n^*_{\alpha\cdot}}{q^*_\alpha}$$

Let $P(i/\alpha)$ be the probability that a fish tagged during the α^{th} period dies and is recovered during the i^{th} recovery period. Now we have C_i fish taken during the i^{th} recovery period to be allocated over the "a" tagging periods, and hence we want the probability that a fish taken during the i^{th} recovery period is one of those which passed the tagging point during the α^{th} tagging period. Denote by $P(\alpha/i)$ the desired probability, and by $P(\alpha)$ the true proportion of the n fish recovered which passed the tagging point during the α^{th} tagging period. Then by Bayes' theorem

$$P(\alpha/i)=\frac{P(i/\alpha)P(\alpha)}{\sum_\alpha P(i/\alpha)P(\alpha)} \quad \ldots\ldots \quad (26)$$

we have the problem of estimating the $P(i/\alpha)$ and the $P(\alpha)$.

Now,

$$P(\alpha)=\frac{\sum_i n_{\alpha i}}{n}$$

and we may estimate $P(\alpha)$ by

$$P^*(\alpha)=\frac{m_{\alpha\cdot}}{m_{\cdot\cdot}} \quad \ldots\ldots\ldots \quad (27)$$

To estimate $P(i/\alpha)$ we may use

$$P^*(i/\alpha)=\frac{m_{\alpha i}}{m_{\alpha\cdot}} \quad \ldots\ldots\ldots \quad (28)$$

Then our estimate of $P(\alpha/i)$ becomes

$$P^*(\alpha/i)=\frac{\frac{m_{\alpha\cdot}m_{\alpha i}}{m_{\cdot\cdot}m_{\alpha\cdot}}}{\sum_\alpha\frac{m_{\alpha\cdot}m_{\alpha i}}{m_{\cdot\cdot}m_{\alpha\cdot}}}=\frac{\frac{m_{\alpha i}}{m_{\cdot\cdot}}}{\frac{m_{\cdot i}}{m_{\cdot\cdot}}}=\frac{m_{\alpha i}}{m_{\cdot i}} \quad \ldots \quad (29)$$

This gives us for an estimate of $n_{\alpha\cdot}$

$$n^*_{\alpha i}=\sum_i C_i P^*(\alpha/_i)=\sum_i C_i\frac{m_{\alpha i}}{m_{\cdot i}} \quad \ldots \quad (30)$$

TABLE 3.—*Data from a tagging experiment on migrating adult sockeye salmon*

	Week of tagging (α)								Total tagged fish recovered	Total fish recovered	$C_i/m{\cdot}i$
	1	2	3	4	5	6	7	8			
Week of recovery (i):									$m{\cdot}i$	C_i	
1	1	1	1						3	19	6.33
2		3	11	5					19	132	6.95
3	2	7	33	29	11				82	800	9.76
4			24	79	67	14			184	2,848	15.48
5			5	52	77	25			159	3,476	21.86
6			1	3	2	3			9	644	71.56
7				2	16	10	1	1	30	1,247	41.57
8			1	7	7	6	5		26	930	35.77
9				3	3	2			8	376	47.00
Total tagged fish recovered $m\alpha$	3	11	76	180	183	60	6	1	520		
Total fish tagged $T\alpha$	15	59	410	695	773	335	59	5			
$T\alpha/m\alpha{\cdot}$	5.00	5.36	5.39	3.86	4.22	5.58	9.83	5.00			

$\Sigma C_i = 10,472.$
$\Sigma T\alpha = 2,351.$

Taking our estimate of $q\alpha$ as before (23), and as our estimate of N

$$N^* = \sum_{\alpha} \frac{n^*_{\alpha i}}{q^*_{\alpha}} \quad \ldots\ldots\ldots \quad (31)$$

we have, then,

$$N^* = \sum_{\alpha}\sum_{i} C_i \frac{m_{\alpha i}}{m_{\cdot i}} \frac{T_\alpha}{m_{\alpha\cdot}} \quad \ldots\ldots \quad (32)$$

which is the same result as obtained in formula 25.

Application of this method of population estimation may be illustrated by the data from a tagging experiment conducted by me on a migrating population of adult sockeye salmon in British Columbia. A total of 2,351 fish were tagged in a certain river, on the way to their spawning grounds, over an 8-week period. Later, tag-ratio samples were drawn regularly over a 9-week period as the fish spawned and died on the spawning grounds farther upstream: 10,472 fish, of which 520 had been tagged, were recovered in these samples. In table 3 are tabulated, in the same form as the table on page 200, tag recoveries by week of tagging and week of recovery, with data on total numbers tagged and recovered for each week. From these data are computed values of $T_\alpha/m_{\alpha\cdot}$ and $C_i/m_{\cdot i}$ tabulated along the margins. From these computed values and the tag-recovery data tabulated in the body of the table has been computed the estimate of the population, as shown in table 4, according to formulae 24 and 25 (or 32). The values in the body of this table are values of $n^*_{\alpha i} = m_{\alpha i} \frac{T_\alpha}{m_{\alpha\cdot}} \frac{C_i}{m_{\cdot i}}$ which sum to the estimate of N, 47,860 fish.

TABLE 4.—*Computation of population estimate by formulae 24 and 25 from the data of table 3*

	Week of tagging (α)								Total
	1	2	3	4	5	6	7	8	
Week of recovery (i):									
1	32	34	34						100
2		112	412	134					658
3	98	366	1,736	1,093	453				3,746
4			2,002	4,720	4,377	1,209			12,308
5			589	4,388	7,103	3,049			15,129
6			386	829	604	1,198			3,017
7				321	2,807	2,320	409	208	6,065
8			193	967	1,057	1,198	1,758		5,173
9				544	595	525			1,664
Total	130	512	5,352	12,996	16,996	9,499	2,167	208	47,860

From formula 25 (or 32) it may be seen that where the tagging or the sampling is uniform, this estimate reverts to the simple case first discussed. For, if the probability of being tagged is constant for all i, the expected value of $\frac{C_i}{m_{\cdot i}} = \frac{n}{m_{\cdot\cdot}}$, a constant. Then,

$$N^* = \sum_{\alpha}\sum_{i} m_{\alpha i} \frac{T_\alpha}{m_{\alpha\cdot}} \frac{n}{m_{\cdot\cdot}} = \frac{T_n}{m_{\cdot\cdot}} \quad \ldots \quad (33)$$

which is identical with formula 1 since $m_{\cdot\cdot} \equiv t$ in formula 1.

Likewise, if the probability of being recovered is constant, the expected value of $\frac{T_\alpha}{m_{\alpha i}}$ is $\frac{T}{m_{\cdot\cdot}}$, a constant. Then,

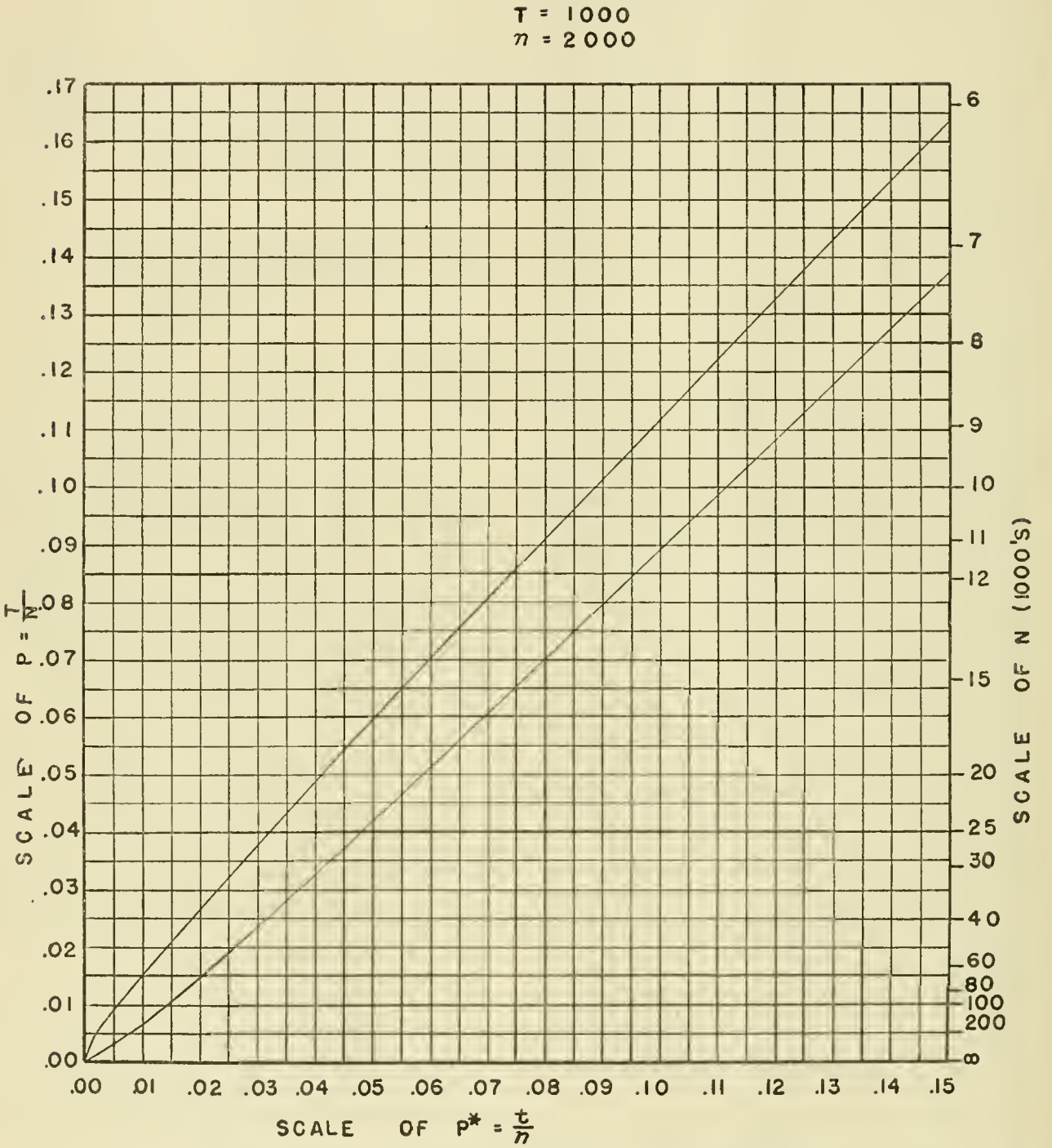
$$N^* = \sum_{\alpha}\sum_{i} m_{\alpha i} \frac{C_i}{m_{\cdot i}} \frac{T}{m_{\cdot\cdot}} = \frac{T_n}{m_{\cdot\cdot}} \quad \ldots\ldots \quad (34)$$

The tagging experiment illustrated in table 3 is a practical situation of this sort. Although the probability of a fish being recovered, estimated from $C_i/m_{\cdot i}$, changed very much during the course

of the season, the probability of being tagged, judged from T_α/m_α, was fairly even over most of the season. In consequence, the estimate from the simple formula (1)

$$N=\frac{(10{,}472)(2{,}351)}{520}=47{,}345$$

is practically identical with the estimate from formula 25 (or 32).



Confidence limits on sample tag ratios and on estimated population numbers, at a confidence level of 95 percent, for experiments involving 1,000 tagged individuals and samples of 2,000.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

AGE, GROWTH, AND PRODUCTION OF YELLOW PERCH IN LAKE ERIE

By Frank W. Jobes

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CONTENTS

	Page
Commercial production of yellow perch in Lake Erie	205
Materials and methods	211
Determination of age and growth of Lake Erie yellow perch by the scale method	214
Validity of the annulus as a year mark	214
Body-scale relation	215
Calculation of growth	218
Calculated growth histories of the age groups	218
Discrepancies in the calculated growth histories of different age groups	220
Selection by gear	220
Segregation correlated with sexual maturity	221
Selective destruction according to the legal size limit	222
Other causes	223
General growth curves	223
Growth in length	223
Growth in weight	224
Growth of yellow perch in Lake Erie compared with that in other waters	227
Growth compensation	229
Proportion of season's growth completed at time of capture	230
Annual fluctuations in growth	232
Length-frequency distribution	236
Age composition and abundance of year classes	243
Length-weight relation	252
Coefficient of condition (K)	253
Monthly and annual fluctuations in the value of K	254
Fluctuations in value of K with stage of maturity	256
Fluctuations in value of K with age	256
Influence of rate of growth on value of K	257
Effect of type of gear on determining value of K	258
Size at maturity	259
Sex ratio	260
Summary	262
Bibliography	264

AGE, GROWTH, AND PRODUCTION OF YELLOW PERCH IN LAKE ERIE

By FRANK W. JOBES, *Fishery Research Biologist*

The American yellow perch, *Perca flavescens* (Mitchill), is one of the most common food fishes native to the lakes and streams of the northeastern United States and southeastern Canada. It contributes heavily to the take by hook and line throughout its range and forms an important part of the catch of the modern commercial fishery in the Great Lakes.

The present study of the yellow perch is part of an extensive investigation of the Lake Erie commercial fisheries begun by the former U. S. Bureau of Fisheries and continued by the U. S. Fish and Wildlife Service. In the years 1927 through 1931 field work was carried on in cooperation with the States of Ohio, Pennsylvania, and New York, the Province of Ontario, the city of Buffalo, and the Buffalo Society of Natural Science; materials were collected also in 1932, 1934, and 1937, and in the years 1943 through 1948. This report is based primarily on the data for the specified years from 1927 to 1937 (referred to here as 1927–37) because in each of those years the materials consisted of random samples of all yellow perch taken by the nets. The 1943–48 data are from random samples of the commercial catch only (fish 8½ inches or more in total length) and will be used only where they add to the knowledge gained from the 1927–37 data.

The assistance of the officials and employees of all the agencies involved in this investigation is deeply appreciated. Without their cooperation in the collection of data and the loan of materials this study would have been much more restricted in scope, if not impossible. Special thanks are due Dr. John Van Oosten for directing the study and critically examining the manuscript, and Dr. Ralph Hile for substantial assistance in the analysis and interpretation of the data. N. H. Lagerstrom, Oberlin, Ohio, translated the Swedish and Norwegian references listed in the bibliography.

Several authors have studied the age and growth of the yellow perch without making a critical study of the validity of age determinations based on scales. Jobes (1933) and Schneberger (1935) calculated lengths from scale measurements on the assumption that the ratio of body length to scale length is constant after the first annulus is formed. Hile and Jobes (1941) determined the body-scale relation for the yellow perch in Saginaw Bay (Lake Huron) and corrected the lengths computed by direct proportion to conform to the empirically determined body-scale relation. Before a detailed study of the life history of the yellow perch in Lake Erie could be undertaken, it was necessary to demonstrate that ages read from scales are accurate and to determine the most satisfactory method of calculating growth from scale measurements.

COMMERCIAL PRODUCTION OF YELLOW PERCH IN LAKE ERIE

The earliest records of the production of yellow perch in Lake Erie are for the year 1885. The species was taken commercially before that time but was not considered important enough to warrant separate treatment in the earlier statistical reports. Table 1 gives the available figures on production for the years 1885 to 1947. The production records for United States waters, for Ontario waters, and for the entire lake are shown graphically in figure 1.

Although the record of the catch in the United States waters is not complete for the earlier years of the fishery, the annual yield appears to have been greater before 1900 than in the period immediately after. The extremes in the fluctuation in annual production during the earliest period, 1885–99, occurred in the years 1885 and 1889, when catches of 1,601,000 and 3,830,000 pounds were reported. The fragmentary statistics indicate a good production in this period; the average

TABLE 1.—*Annual production of yellow perch in Lake Erie, 1885–1947*

[In thousands of pounds]

Year	United States [1]					Canada (Ontario) [2]			Entire lake
	Michigan	Ohio	Pennsylvania	New York	Total	Western part [3]	Eastern part [4]	Total	
1885	100	1,266	225	11	1,601				
1886									
1887									
1888									
1889	96	3,204	459	70	3,830				
1890	159	2,483	209	49	2,900				
1891									
1892	138								
1893	223				2,595				
1894	115					282	281	563	
1895	255					241	156	397	
1896	202					266	208	474	
1897 [5]	147	2,604	407	95	3,253	238	263	500	3,753
1898	164					121	258	379	
1899	92	2,175	816	258	3,340	209	182	391	3,731
1900	128					398	297	695	
1901	136					255	253	508	
1902	107					373	193	566	
1903	81	625	141	27	873	218	201	418	1,292
1904	70					436	161	598	
1905	106					346	207	553	
1906	99					176	158	334	
1907	118					364	108	472	
1908	147	1,441	85	83	1,756	450	180	630	2,386
1909						428	153	581	
1910						464	210	674	
1911						681	167	847	
1912	85					913	198	1,110	
1913	66	[6] 685	[7] 114	4	870	794	161	955	1,825
1914	57	1,888	81	13	2,039	1,137	271	1,408	3,447
1915	108	1,698	105	22	1,933	809	234	1,042	2,975
1916	136	1,370	115	17	1,637	614	155	769	2,406
1917	140	866	173	79	1,259	852	143	995	2,254
1918	68	919	80	21	1,088	1,810	246	2,056	3,145
1919	37	2,573	51	114	2,775	876	221	1,097	3,872
1920	42	1,189	18	10	1,259	1,005	267	1,272	2,532
1921	41	2,053	70	28	2,192	1,676	289	1,965	4,157
1922	68	1,758	54	47	1,926	1,810	299	2,109	4,035
1923	36	1,668	98	67	1,870			2,397	4,267
1924	34	[8] 1,677	199	31	1,941	1,719	473	2,192	4,133
1925	48	2,202			2,458	1,304	756	2,060	4,518
1926	63	2,414	76	68	2,622	1,323	393	1,716	4,338
1927	32	2,468	206	40	2,748	1,888	603	2,491	5,238
1928	20	3,678	447	130	4,275	3,577	753	4,330	8,606
1929	35	5,779	177	52	6,043	4,782	907	5,689	11,733
1930	34	4,187	85	34	4,341	2,839	580	3,420	7,761
1931	72	8,455	480	55	9,062	3,466	799	4,265	13,327
1932	97	9,239	330	75	9,741	3,657	1,372	5,029	14,770
1933	87	3,024	278	45	3,434	1,474	1,255	2,729	6,163
1934	48	13,252	798	119	14,218	3,460	2,211	5,671	19,889
1935	54	8,303	542	146	9,045	3,795	1,838	5,634	14,678
1936	17	1,885	131	18	2,051	887	367	1,254	3,305
1937	16	1,596	105	34	1,750	1,298	393	1,691	3,441
1938	25	4,912	200	50	5,187	2,139	457	2,596	7,782
1939	13	1,493	80	21	1,608	956	451	1,407	3,015
1940	14	2,774	216	25	3,030	1,390	604	1,994	5,024
1941	25	3,596	163	38	3,821	1,398	652	2,050	5,871
1942	36	1,790	89	44	1,958	640	324	964	2,922
1943	24	1,178	31	20	1,253	536	175	711	1,964
1944	20	2,092	56	20	2,188	1,146	226	1,372	3,560
1945	29	1,260	58	5	1,352	982	225	1,207	2,559
1946	46	2,535	95	8	2,685	2,110	307	2,417	5,102
1947	49	1,587	97	63	1,797	1,454	798	2,252	4,049

[1] Records of production from United States waters and from entire lake for 1885–1940 are from Gallagher and Van Oosten (1943). Statistics of production from United States waters for later years were compiled originally in the Great Lakes Laboratory of the U. S. Fish and Wildlife Service from data supplied by the several States and have been published in the Commercial Fishery Statistics series of the Service.

[2] Canadian (Ontario) records for 1894–1939 are from Ford (1943). Data on the yield from Canadian waters in later years were supplied by the Ontario Department of Lands and Forests. The figures on the catch from all of the Canadian waters of Lake Erie may be found in the annual reports of the Ontario Department of Lands and Forests.

[3] West end to Port Burwell.

[4] East of Port Burwell.

[5] Fiscal year, July 1, 1896, to June 30, 1897, in United States waters, except Michigan.

[6] Fall catch only.

[7] Estimated.

[8] Fall catch of 1924 plus spring catch of 1925.

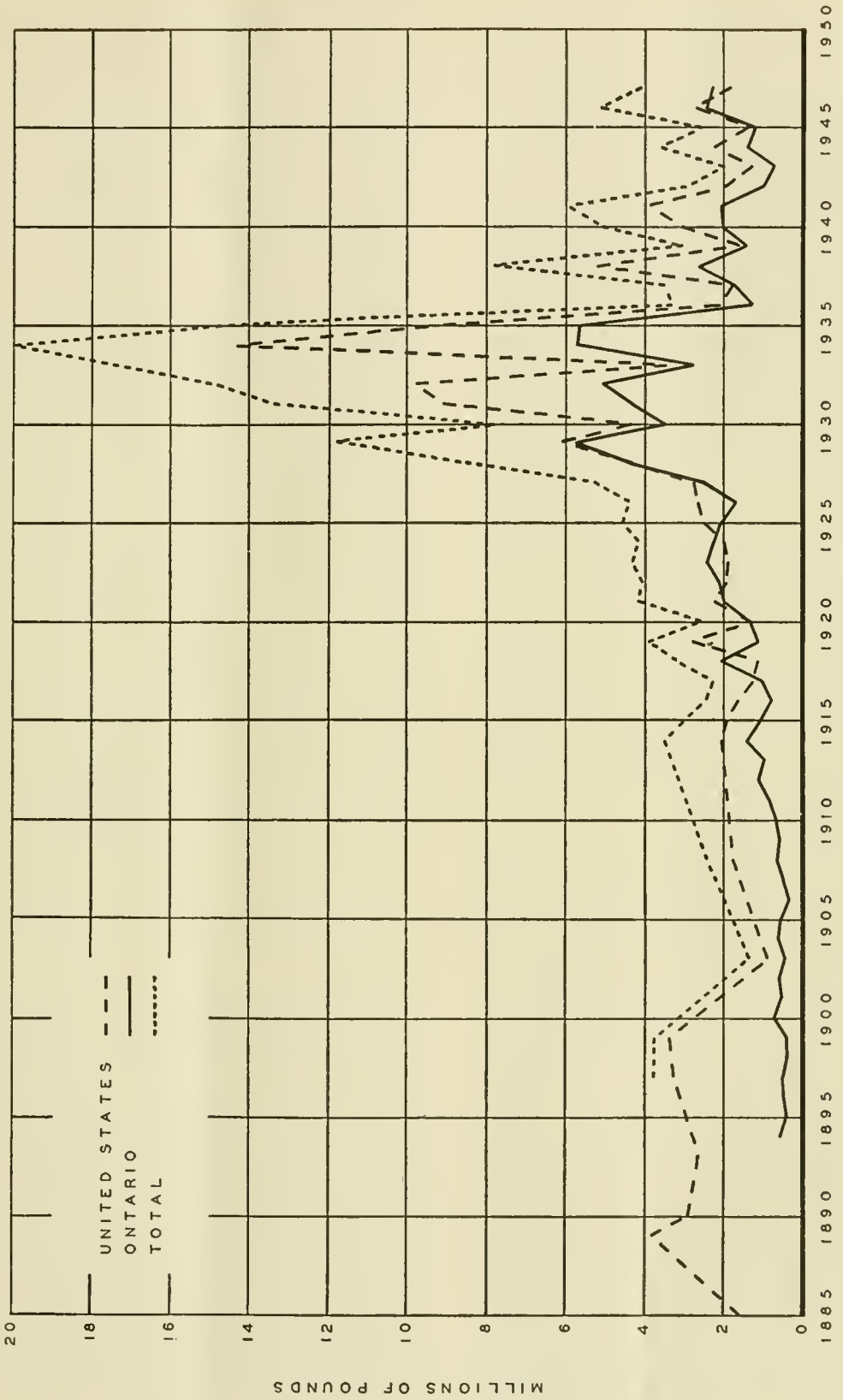

FIGURE 1.—Annual production of yellow perch in Lake Erie, 1885–1947

of the recorded yields was 2,946,000 pounds.[1] The lowest annual United States yield on record occurred in the next period, 1900–1927, when in 1903 only 873,000 pounds were reported. (No reference has been found that suggests that the statistics for 1903 are incomplete.) In only 6 years (1914, 1919, 1921, 1925, 1926, and 1927) of the 16 in this period did the annual catch from United States waters exceed 2 million pounds. The average annual yield of 1,905,000 pounds in this period was only 65 percent of the 1885–99 average. The upward trend that was to carry the yield in United States waters to the unprecedented catch of nearly 14¼ million pounds in 1934 actually began in 1925, but was relatively slight until 1928. The average of 7,520,000 pounds for the years 1928–35 was 2.55 times the average of the 1885–99 period and 3.95 times the 1900–1927 average. Not only was production high in 1928–35, but the fluctuations in annual catch were sudden and violent (for example, 9,741,000 pounds in 1932, 3,434,000 pounds in 1933, and 14,218,000 pounds in 1934). The violent fluctuations continued into the 1936–47 period, when the average annual production fell to 2,390,000 pounds. The average annual yield in these most recent years was 81 percent of that of the 1885–99 period, and only 32 percent of the 1928–35 average. The grand average for the years of recorded statistics was 3,262,000 pounds.

The Ohio production has always dominated the United States catch, and in the years for which complete data are available Ohio, on the average, has accounted for more than half of the yield of the entire lake. Furthermore, the relative importance of the Ohio catch in the United States production has shown a distinct tendency to increase. In the early period, 1885–99, Ohio produced 77.8 percent of the total United States yield. This percentage increased to 87.7 in the 1900–1927 period, to 92.9 in 1928–35, and to 93.1 in recent years. The proportion of the United States catch taken in each of the three remaining States has tended to decline.

If the Ontario statistics were to be segregated by periods independent of those of the United States, the following intervals would be selected to show the trend of production: 1894–1911, 1912–20, 1921–27, 1928–35, and 1936–47. The Ontario figures in table 1 show a progressive increase in catch with each succeeding period except the last. This trend on the Canadian side of Lake Erie, therefore, does not correspond to that on the United States side, except during the last two periods, 1928 and following years. Apparently the Canadian fishery for yellow perch began later and developed more slowly than that of the United States.

The earliest statistics of the catch in Ontario waters of Lake Erie show a relatively low yield with no extremely large variation from the average of 532,000 pounds during the period 1894–1911. The average annual catch of the next period, 1912–20, was 1,189,000 pounds or 2.23 times the 1894–1911 average; in only one year, 1918, did the take exceed 1½ million pounds. The 1921–27 period was one of relatively stable production with an average catch of 2,133,000 pounds (1.79 times the average of the preceding period). The large annual catches and increased variability of the annual yields in Ontario waters in 1928–35 were not unlike those in United States waters for the same period, except that in Ontario production did not reach such heights and the fluctuations in catch were not so violent as in the United States. The average annual Ontario yield for this period was 4,596,000 pounds, or 2.15 times that of the preceding period. Production during 1936–47 declined to an average of 1,660,000 pounds, or to 36 percent of the 1928–35 average. In only 4 of the last 12 years, 1938, 1941, 1946, and 1947, did the catch exceed 2 million pounds. The grand average for the 54 years of recorded statistics was 1,702,000 pounds.

The production from the western part of the lake (west end to Port Burwell), on the average, made up more than 60 percent of the Canadian total in each period. The percentage increased from 62 in the years 1894–1911 to 82 in 1912–20, and remained relatively constant, between 74 and 78, in the last three periods. This stabilization in the relative productivity of the two sections of the Canadian waters is in contrast to the situation in the United States waters where the western (Ohio) section increased in importance each period.

The catch in the entire lake showed variations similar to those in United States waters, except during the years 1921–27, when the total production was augmented by the increased yield in

[1] To make use of all available statistics, the averages computed from table 1 for United States waters, and for the entire lake, are the sums of the corresponding averages of the individual States and the Province of Ontario.

Ontario waters. The average total production of about 3⅓ million pounds during the period 1885–99 appears high only when consideration is given the low fishing intensity and the crude apparatus employed. The output of the fishery was low in 1903 but tended to increase, though irregularly, during the 1900–1920 period. The average annual yield of 2,464,000 pounds during this period was approximately 70 percent of the earlier average. The following period, 1921–27, was the steadiest one of the fishery, with but little fluctuation from an average of 4,384,000 pounds. This average was 1.78 times the average of the preceding period and about 1.29 times the 1885–99 average. The period 1928–35 was one of tremendous annual productions and violent fluctuations in yield from year to year. In every year, the catch exceeded the best of any previous period, and in 5 of the 8 years it was more than 10 million pounds. The average annual catch of 12,116,000 pounds was 4.92 times the 1900–1920 average and 2.76 times the 1921–27 average. During 1936–47, production fell off, with only one year, 1938, yielding as much as the poorest of the preceding period. Wide fluctuations in yield persisted into this last period. They were caused largely by variations in the catch in United States waters, and these in turn were due to variations in Ohio's yield. The average catch of 4,050,000 pounds in 1936–47 was only about a third of the 1928–35 average but was approximately 1.25 times the average of the earliest period, 1885–99.

The grand average production of yellow perch in all waters of Lake Erie for the years 1885 to 1947 was 4,964,000 pounds.

The tendency toward an increasing variability in the annual catch in United States waters suggests the dependence of the commercial fishery on a small number of age groups. This interpretation is supported by the observation (p. 245) that in the present-day fishery a year class is normally of major importance for little longer than a single year. Under such conditions it may be expected that production would be sensitive to variations in the strength of year classes and hence subject to sudden and wide fluctuations.

Any discussion of the factors that contributed to the changes that have occurred in the production of yellow perch in Lake Erie must be in large measure speculative. Although certain events are known to have contributed to the observed changes, their precise effects are difficult to evaluate. Brief mention may be made of the more important factors.

The early fishery in Lake Erie was conducted primarily on the inshore grounds with relatively crude gear. As production on these grounds declined, larger, faster, and seaworthier boats were built which permitted not only the extension of operations to more distant grounds but also the handling of more nets. The number of boats in operation also increased rapidly with expansion of the fishing grounds. Further increase in the amount of gear handled by each boat followed introduction of the power lifter for gill nets in the 1890's and for trap nets in the early 1930's. Efficiency of the nets was increased by reducing the size of the meshes, by using finer thread in gill nets, and by "reefing" or tying down the gill nets. Gill nets were made still more efficient by the development of the bull net, a gill net 100 meshes deep, fished in all strata of water from top to bottom. The shift from pound nets to trap nets and more recently a partial shift from gill nets to trap nets also increased exploitation, since trap nets are the most efficient gear now in use.

Although it is not possible to state precisely the extent to which fishing intensity has increased, it is valid to state that the increases in the amount and efficiency of gear just mentioned have led to a multiplication of fishing intensity in recent years over that of the early fishery.

For many years the practice has been to decrease gradually the size of mesh in the nets to compensate for diminishing yields. It was not until 1937 that the State of Ohio reversed the trend by increasing the size of mesh in trap nets to afford greater protection to the smaller fish.

In addition to these developments that have affected the fishery as a whole, there have been other circumstances that contributed more specifically to an increase in the intensity of the fishery for perch. The collapse of the cisco fishery, formerly the most productive in Lake Erie, in 1925 forced many operators, particularly the gill-netters, to turn to other species. The resulting increase in intensity of the fishing for perch was an important factor in the rise in production of this species. The yield of perch was affected also by the reduction in July 1929 of the minimum legal size from 9 to 8½ inches in the State of Ohio. The record catch of 13 million pounds in Ohio in 1934 oc-

curred in a year when the officials failed to enforce the law on size limits.

Economic conditions doubtless have had an effect on the annual fluctuations in the yield of perch, but the relation is too obscure to point to any major change in the annual catch as the result of changes in the price of or demand for perch.

The discussion of the relation of production to fishing intensity, to fishery laws and enforcement of laws, and to market conditions, has been given in advance of the treatment of the relation between the catch and the abundance of perch, not with the intent to imply that abundance is not of great importance in determining the yield, but rather to bring out the dangers of interpreting too freely fluctuation in production as the result of fluctuation in abundance. To be sure, abundance and catch are closely related; but careful recognition also must be given to other factors that affect the annual yield.

Abundance may be considered in terms of long-period changes such as those brought about by the prosecution of the fishery or by gradual changes in the environment, or in terms of the short-period fluctuations traceable to variations from year to year in the success of natural reproduction. Both types of changes are reflected in fluctuations in the annual catch. Many of the variations in annual yield as recorded in table 1 are probably to a large extent the result of relative strength or weakness of year classes. Age determinations have shown, for example, that the increases in production in 1928 and 1929 were not exclusively the result of increased fishing intensity and the reduction of the legal size for perch, but were furthered also by the phenomenal richness of the 1926 year class.

The fluctuations in abundance that arise from variations in the strength of year classes must be accepted by fishermen as part of the natural course of events, since at present very little can be done to increase the survival of young. The environment may be improved by such measures as the control of pollution and erosion. The value of such measures to the Lake Erie fisheries is open to question, since it has been shown that no extensive areas of heavy pollution exist that would be inimical to fish life (Wright and Tidd 1933, Fish 1929), and that turbidity is not a factor in either the survival of the young or their subsequent growth in Lake Erie (Van Oosten 1948). In fact, the causes underlying annual variations in the success of natural reproduction are little understood. Although a knowledge of the fluctuations that occur in the strength of year classes may contribute to an understanding of changes in the fishery, a knowledge of the general level of abundance and of long-period trends in abundance is more pertinent to the solution of administrative problems than is information on short-period fluctuations.

The abundance of yellow perch in the early period of the United States fishery (1885–99) must have been at a relatively high level, since good production was maintained in spite of low fishing intensity and inefficient methods. On the other hand, the reduced yields of the 1900–1927 period—one of expanding fishing intensity and increasing efficiency in fishing methods—indicate a sharp reduction in the general level of abundance. The greatly increased production in 1928–35 must be considered the result, in part at least, of the increase in intensity of the fishery for perch that followed the collapse of the cisco fishery. The known abundance in 1928 and 1929 of perch of the big 1926 year class and the virtual removal of the size limit in Ohio in 1934 undoubtedly contributed to the large yields in those years. It seems unlikely, however, that a production of over 14 million pounds could have been reached in 1934, even without a size limit, unless the population had reached an enormous size that year. Likewise, the yields of more than 9 million pounds in 1931, 1932, and 1935 indicate tremendous abundance. Evidence will be presented later (p. 245) which shows that normally the perch of a year class dominate the fall fishery in their third year and the spring fishery in their fourth year of life. Thus, two year classes of perch make up the bulk of the commercial catch each calendar year. On the basis of that evidence, it may be assumed that the year classes of 1928 to 1932 or 1933, inclusive, were of exceptional strength to have been able to produce the high yields during the period 1931–35.

The statistics (table 1) suggest strongly that the abundance of yellow perch was reduced greatly during the years 1936–47. The fishing intensity may have decreased in United States waters when some of the operators quit business, but it is known also that some new outfits started operations during this period. Increase in size of the mesh in the Ohio trap nets probably did not

release enough legal-sized perch to affect materially the total yield. Since Van Oosten (1932) showed that trap nets with a mesh larger than that employed in the nets at the present time did not release perch of 8½ inches (present legal size limit) and larger, the reduction in take in 1936–47 undoubtedly was largely the result of a decrease in abundance of perch rather than a decrease in fishing intensity.

A precise evaluation cannot be made of the changes in abundance of the yellow perch in Lake Erie during the period of greatest fluctuations in yield, because the data are not sufficient. An approximation of the abundance may be obtained, however, from the records of the W. D. Bates Fishery, Rondeau, Ontario, which give the number of pound nets fished and the catch each year for the period 1900–1940, and from those of Leonard Bickley, Sandusky, Ohio, which give the catch by trap nets of a 1-boat fishery during the years 1911–31. The records of number of nets fished and total pounds of fish taken published by the former Ontario Department of Game and Fisheries also are of value.

Although there are certain discrepancies among these three sets of data, they all suggest that the period 1928–35 was one in which the abundance of yellow perch in Lake Erie was high, and all data are consistent in showing that the abundance declined sharply in 1936 and has remained at a relatively low level since that time. Bickley's data, in contrast to those of Bates, suggest a slight increase in abundance in 1921–27, thus indicating that the slight rise in production in the Ohio waters in those years may, in part, reflect abundance.

It must be recognized that the yellow-perch fishery in Lake Erie is not in a prosperous condition at the present time. That the fishery has not collapsed entirely is perhaps a tribute to the fecundity of the perch. The danger exists in the absence of a reserve supply, as well as in the low abundance. The failure of only two successive year classes would lead to collapse of the fishery.

MATERIALS AND METHODS

Materials for this investigation on the age and growth of yellow perch were collected at the following Lake Erie ports: Port Clinton, Sandusky, Huron, Vermilion, Lorain, Ashtabula, and Conneaut, Ohio; Erie, Pa.; and Dunkirk, N. Y. (See fig. 2.) Originally a separate analysis was made of the data for yellow perch from the western, middle, and eastern sections of the lake; it was found, however, that a combination of the data was justifiable. It was found also that the data for trap nets and pound nets could be combined.

Table 2 shows, for each type of gear, the number of specimens on which this study has been based. The 1927–37 materials used in the growth-rate studies, a total of 3,036 fish, were random samples of the trap-net and pound-net catches taken during the latter part of the collecting period of each year. Samples from impounding nets were used because that type of net is less selective than gill nets, and because the impounding-net collections covered a greater period of years. The 1,341 fish taken from trap nets in the years 1943–48 were used in the study of annual fluctuations in growth. The ages were determined of 430 specimens taken in commercial gill nets during 1927 and 1928, and of 1,136 fish taken in the years 1943–48. The 1927–28 material consisted of random samples from shoal nets (228 fish) and from bull nets (202 fish). The data on age were used to compare the age composition of the catch in gill nets with that of impounding nets.

All specimens for which length and weight were recorded (23,158 fish) in 1927–37 were used in the study of the length-weight relation. The length-frequency data for the years 1927–37 were based on 58,665 specimens taken from random samples only and included those specimens whose ages were determined, most of those used in the study of the length-weight relation, and a large number for which lengths only were obtained. The length distribution of 1,114 yellow perch taken in 1943–48 by trap nets was used for comparison with the earlier material.

Investigation of the relation between scale length and body length was based on the examination of selected or "key" scales from 600 specimens collected in western Lake Erie as follows: September to November 1928, 188; May to August, and November 1929, 79; October 4, 1934, 207; April 1937, 60; and late autumn 1937, 66. The scale measurements from only 576 of these specimens could be used, since 24 individuals had lost the designated scale or had key scales that were regenerated, injured, or otherwise atypical. The

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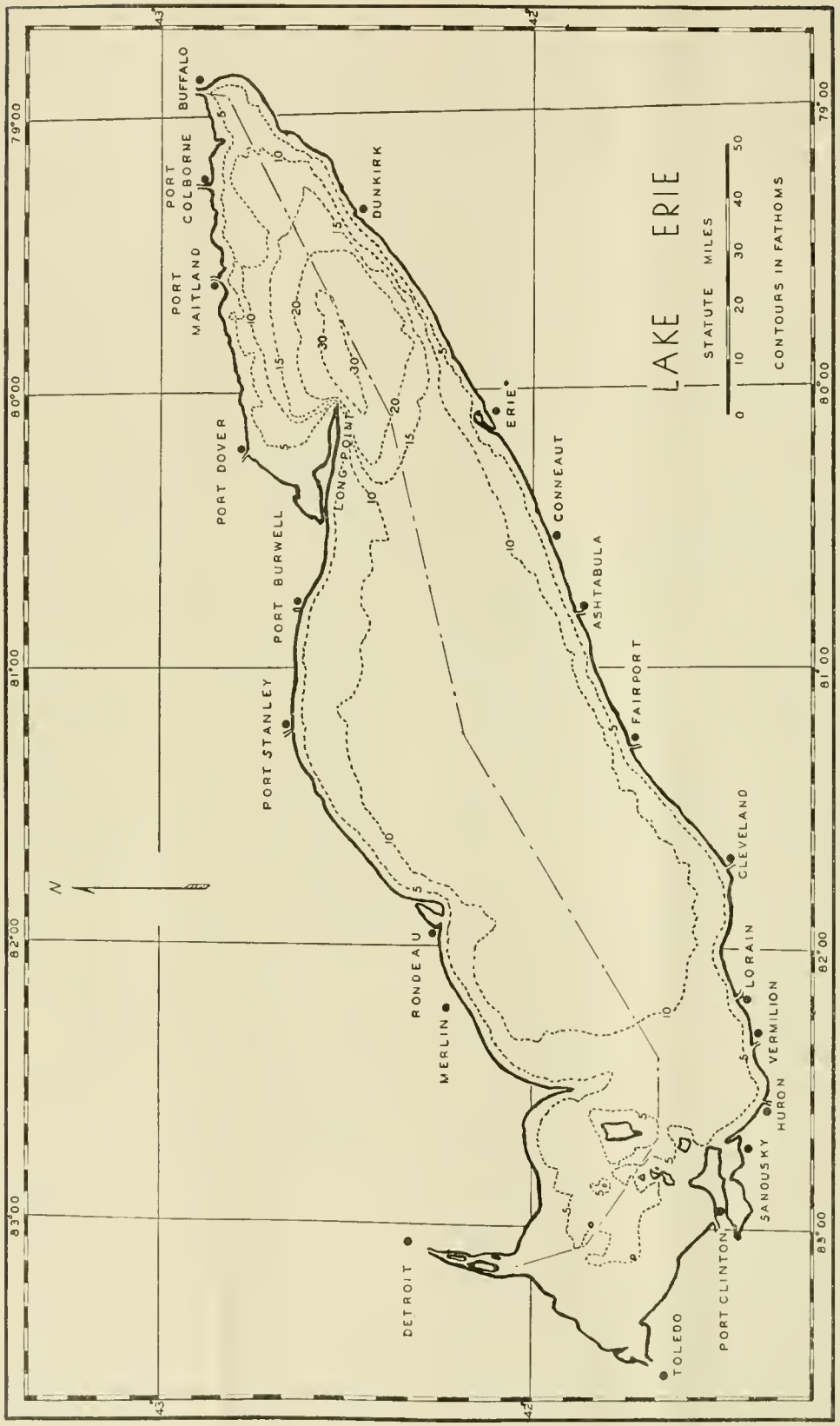

FIGURE 2.—Lake Erie.

TABLE 2.—*Specimens used in study of Lake Erie yellow perch and gear employed in taking them*

Gear employed and year taken	Number of specimens used in study of—		
	Age and growth	Length-weight relation	Length frequency
Caught by impounding net during—			
1927	481	1,516	3,224
1928	[1] 918	3,123	5,785
1929	[2] 1,151	11,215	11,939
1930	222	269	7,118
1931			19,391
1932	133	133	133
1934	[3]	207	
1937	[4] 131	131	131
1943	45		
1944	81		81
1945	157		132
1946	225		204
1947	343		297
1948	490		400
Total	[5] 4,377	16,594	48,835
Caught by shoal gill net [6] during—			
1927	84	1,659	1,670
1928	144	3,386	2,754
1929			4,744
1930			
1931			
1932			
1934			
1937			
1943	129		
1944	57		
1945	75		
1946	204		
1947	380		
1948	291		
Total	1,364	5,045	9,168
Caught by bull gill net [7] during—			
1927	69	116	257
1928	133	565	681
1929		838	838
1930			
1931			
1932			
1934			
1937			
1943			
1944			
1945			
1946			
1947			
1948			
Total	202	1,519	1,776
Grand total	5,943	23,158	59,779

[1] In addition, 188 selected specimens were used in the key-scale study.
[2] In addition, 79 selected specimens were used in the key-scale study.
[3] 207 selected specimens were collected for key-scale study.
[4] In addition, 126 selected specimens were used in the key-scale study.
[5] Selected specimens used in the key-scale study and for the determination of maximum age are not included in the totals.
[6] Gill nets 22 meshes deep.
[7] Gill nets 100 meshes deep.

600 specimens collected for the key-scale study were not used for any other purpose, except the 207 collected October 4, 1934, which were employed as part of the data on the length-weight relation.

During 1927 and 1928 the lifting cribs of the trap nets from which samples were taken were made of 2-inch or 2¼-inch webbing (stretched measure as manufactured), except for the vertical middle third of the backs, where the mesh was 2⅞ inches. From 1929 to 1937 the mesh of the crib was 2¼ inches (stretched measure as manufactured) in all parts except the entire back where the mesh was 2¾ inches. Since 1937 the mesh in the back of trap nets has been 2⅞ inches, with the sides made of 2½-inch mesh. The pound-net samples (from Erie, Pa.) were from nets with meshes of $2\frac{11}{16}$ inches (stretched measure as manufactured). The gill nets, from which the 1927–28 samples were studied, were of 3-inch and $3\frac{1}{16}$-inch mesh (stretched measure as manufactured). Since the length frequencies of the perch taken in the two sizes of mesh showed no significant differences, the size of mesh was ignored in treating the gill-net data. The gill-net data, however, have been separated on the basis of depth of net because there was a difference between the length frequencies of perch taken in shoal gill nets and in bull gill nets. The shoal nets were 22 meshes deep and the bull nets 100 meshes deep. The meshes of the shoal nets from which the 1943–48 samples were taken measured 2⅞ inches.

Except in 1930–31 and 1943-48, lengths were measured with a flexible steel tape held so as to follow the curve of the body from the tip of the snout to the thickest part of the body, and then in a straight line approximately parallel to the long axis of the body. The length records of fish caught in 1930–31 and 1943–48 were obtained with a measuring board. The lengths measured on the board were converted to "tape-line lengths" by the factor 1.02. Weights were recorded to the nearest fourth of an ounce except in 1948 when they were recorded in tenths of ounces. All measurements of length and weight were obtained from fresh specimens in the field, except those of fish collected for key-scale study. Of those, the 207 used in the length-weight-relation study were shipped fresh, packed in ice, to the laboratory, where they were measured and weighed, and the rest, all preserved, were measured but not weighed. Lengths obtained from preserved specimens were corrected for shrinkage produced by the preservative; the correction factor was 1.0065.

Scales for age determinations were taken from the left side of the fish, below the lateral line and beneath the spinous dorsal fin. They were mounted on standard glass microscope slides in

the gelatin-glycerin medium recommended by Van Oosten (1929).

The first examinations of the 1927 and of part of the 1928 scale collections were made by use of the projection apparatus described by Van Oosten (1923). The final examinations and the measurements of those scales, and all examinations and the measurements of the remaining scales, were made by means of the apparatus described by Van Oosten, Deason, and Jobes (1934) at magnification × 40.7. The measurements from the focus to each successive annulus and to the extreme edge of the scale were made along the most anterior interradial space. Approximately 5 percent of the scales examined were discarded because the age could not be determined with confidence.

Ages are designated in roman numerals corresponding to the number of annuli visible on the scales except for those fish taken in the early spring before growth began. An annulus was assumed to be present on the edge of the early-spring scales. Such an assumption is necessary to avoid the assignment of one age to fish of a year class whose scales were without spring growth and another age to fish of the same year class collected the same day whose scales had begun the current season's growth. Thus fish assigned to age group I were in or just ready to begin their second year of life.

DETERMINATION OF AGE AND GROWTH OF LAKE ERIE YELLOW PERCH BY THE SCALE METHOD

Since the demonstration by Hoffbauer (1898) that the age of carp could be determined by examination of their scales, the scales of fish have been used extensively for the study of growth rates and age composition of the stocks of many marine and fresh-water species. Historical summaries of the literature and discussions of the validity of age determinations from scales and of growth calculations from scale measurements already published make it unnecessary to say more here than that the major part of the evidence, obtained from a wide range of species, substantiates the general premise that age can be determined accurately from scale markings and that measurements of fields of growth in scales can be employed for the calculation of lengths at the end of the different years of life.

VALIDITY OF THE ANNULUS AS A YEAR MARK

It has been assumed by the several workers that ages may be determined accurately from an examination of the scales of the American yellow perch, since these scales showed clearly the characteristics that had been used in the accurate determination of the ages of certain other species. The data and observations of the present study, given in the following paragraphs, substantiate this assumption.

1. The collections of 1927, 1928, and 1929 were dominated by fish whose scales showed 1, 2, and 3 annuli, respectively. The corresponding average total lengths of the age groups were 7.5, 8.3, and 9.5 inches. (Most of the 1928 collections were not made as late in the autumn as were the collections of 1927 and 1929; consequently, the average length of 8.3 inches does not represent 3 full years of growth.) That the catches of succeeding years were dominated by progressively larger individuals which, in accordance with expectation, were shown by scale readings also to be progressively older, is strong evidence that one annulus is formed each year and that the scale markings can be interpreted accurately for at least the first three years of life.

2. Scales collected on December 7, 1929, showed no annulus on the edge. Samples obtained July 1, 1929, April 11 and 13, 1932, and April 29, 1937, showed an annulus forming on the edge of the scales. On July 11, 1930, the scales showed a completed annulus a short distance inside the margin. The outermost annulus was farther from the scale margin on September 25, 1930, than in July. These observed variations, especially those on the relative positions of the annulus within the scale margin at different times during the same year (1930), provide evidence that only one annulus was formed on yellow-perch scales each year.

3. There was closer agreement between the calculated and empirical lengths of fish of the same age as determined from scales than between those of different ages. This agreement indicates a constancy in the number of annuli formed each year.

Annulus formation appears to be completed between early April (1932 and 1937 collections) and the middle of July (1929 collection). There is no evidence from these data to show a relation between the time of annulus formation and sex, maturity, or spawning activity. The annulus on yellow-perch scales cannot be said to be a spawning mark despite the approximate coincidence of spawning and the completion of the annulus because (1) immature yellow perch form annuli identical in appearance with those formed by spawning fish, (2) the stage of sexual maturity appears to have no influence on the time of year the annulus is completed, and (3) the annuli do not show the typical spawning marks observed in other species of fish.

The most important characteristics of the annuli on the scales of the Lake Erie yellow perch may be stated briefly to be the "cutting over" in the lateral fields resulting from the discontinuity between scale sculpturing of the successive growth areas, and the irregular or fragmented appearance of the last circulus laid down each year. Usually there is a narrow, clear band between the outermost circulus of one growth area and the first circulus of the next.

False (accessory) annuli occurred not infrequently on the yellow-perch scales but are believed not to have affected the results seriously since all that were recognized were disregarded. Those annuli designated as false were characterized by a decreased amount of "cutting over," by less-well-defined discontinuity between the adjacent fields of growth, and, frequently, by a position that would have given inconsistent calculated lengths.

BODY-SCALE RELATION

Few calculated lengths for the American yellow perch have been published. The earliest, by Jobes (1933) and Schneberger (1935), were computed by the Dahl-Lea method of direct proportion. This method is based on the assumption that the ratio of body length to scale length is constant at all lengths beyond that at which the first year mark or annulus is formed. The age and growth of the closely related European perch, *Perca fluviatilis* L., have been studied by this method by several investigators who found that the lengths calculated by direct proportion usually were less than the empirical lengths for the early years of life.

In spite of the wide use of the direct-proportion method, numerous investigations have shown that this method frequently failed to give satisfactorily accurate results since the computed lengths obtained often did not agree with empirical lengths. Of the several methods developed to obtain a closer agreement between calculated and empirical lengths only that of Segerstråle (1933) for the European yellow perch will be mentioned here, since the calculation of lengths in the present study was by a modification of his procedure.

Segerstråle determined the average scale lengths corresponding to different body lengths through an extensive series of measurements of "key" scales, or "Normalschuppen," taken from a selected area of the body. The body-scale relation so determined, expressed either in tabular form or as a curve, served as the basis for calculating the growth histories of individual fish. On purely theoretical grounds, the method of Segerstråle is the best since it assumes no fixed mathematical relation between body length and scale length, but rather is based on the detailed examination of the actual size of scale at different body lengths. The most serious objection to the use of an empirically determined relation of body length to scale length in the calculation of growth histories is the practical difficulty of obtaining samples with adequate representation of all lengths of fish. The distribution by length of a fish population usually is such that individuals of certain sizes are difficult or impossible to obtain. Inadequate representation of these length intervals inevitably leads to inaccuracies in the calculated lengths.

The diversity of opinions expressed and of results obtained by the several investigators dealing with presumably representative collections of the same and different species leads to the conclusion that the relation of body length to scale length in fishes is not a subject for generalization. The proper method of calculation must be determined for the material at hand. Data on the yellow perch from Lake Erie made possible an analysis, for the first time,[2] of the relation of body length to scale length in a population of American yellow perch.

[2] Although circumstances prevented earlier publication of this study, Hile and Jobes (1941) were able to apply the method developed here to the determination of the body-scale relation of the yellow perch of Saginaw Bay.

Only key (selected) scales were used to determine the relation between size of scale and size of fish. The scale on the left side of the fish in the third row below the lateral line and directly beneath the sixth spine of the dorsal fin was designated the key scale. The position of the key scale approximated the center of the area from which the unselected scales were obtained for age and growth determinations. The scale occupying the designated position on the right side of the specimen was used when the one on the left side was lacking or was regenerated or malformed. Although the collections for the key-scale study were taken at widely spaced intervals of time (see p. 211), an analysis of the data failed to reveal any large or consistent differences for fish captured in different years or seasons.[3] There is no evidence of a seasonal lag between the growths of body and scale in the Lake Erie yellow perch. The data also failed to show any consistent differences in the relative sizes of scale correlated with sex or stage of maturity. Therefore, data from all fish have been combined in this study without regard for the time of capture, sex, or stage of maturity.

Table 3 shows the average standard length of the Lake Erie specimens grouped in 10-millimeter intervals, and the corresponding average total lengths in inches, together with the average scale measurement (at magnification × 40.7), and the body-scale (*L/Sc*) ratios of each length and age group. The *L/Sc* ratios of the age groups are the averages for data collected both at the end of the growing season and at various times throughout the summer (see p. 211). The data were originally grouped in 5-mm. length intervals, but careful examination revealed that condensation to 10-mm. intervals was justifiable. The average *L/Sc* ratios of the age groups indicate that the relative size of the scale increased during the first 3 years of life and then decreased slightly during the fourth. However, a comparison of the *L/Sc* ratios of fish in the same length interval but of different ages revealed that there was no consistent change in the relative size of scale with age. Consequently, the differences between the relative sizes of scales in the different age groups do not depend directly on age but rather on the length distribution of the age groups. Comparisons between fish in the same age group but of different average lengths showed that the *L/Sc* ratios became relatively smaller (relatively larger scales) as the fish length approached 4.3 inches (see data for age groups 0 and I); remained reasonably constant over the length range of 4.3 to 9.2 inches (age groups I, II, and III); and then established another reasonably steady but higher ratio (relatively smaller scales) over the length range of 9.2 to 10.9 inches (age groups II and III).

[3] The scales of group 0 (first year of life) yellow perch caught during late October and early November 1928 were found to be consistently somewhat smaller than the scales from fish of the same length and the same year class that were caught during September 1928 and June 1929. This unusual phenomenon cannot be explained satisfactorily at present. However, the differences were so small that the inclusion of fish caught during October and November did not change greatly the grand average ratio of body length to scale length (table 3).

TABLE 3.—*Body length to scale length ratio (L/Sc) of selected scales from western Lake Erie yellow perch by 10-mm. intervals*

[Number of specimens in parentheses]

Standard-length interval	*L/Sc* ratio for age group—				Grand average *L/Sc* ratio	Average standard length (millimeters)	Average total length (inches)	Average scale measurement (×40.7)
	0[1]	I	II	III				
41 to 50 mm	1.97 (40)				1.97 (40)	47.7	2.3	24.2
51 to 60 mm	1.74 (91)	1.64 (3)			1.74 (94)	55.5	2.7	31.9
61 to 70 mm	1.55 (37)	1.57 (27)			1.66 (64)	64.6	3.1	41.4
71 to 80 mm	1.41 (7)	1.42 (23)			1.41 (30)	74.6	3.6	52.8
81 to 90 mm	1.36 (1)	1.32 (25)			1.33 (26)	85.2	4.1	64.3
91 to 100 mm		1.16 (32)			1.16 (32)	97.2	4.6	83.6
101 to 110 mm		1.15 (15)	1.21 (1)		1.16 (16)	104.2	5.0	90.1
111 to 120 mm		1.19 (6)			1.19 (6)	116.5	5.5	98.2
121 to 130 mm		1.16 (11)	1.11 (1)		1.16 (12)	126.3	6.0	110.2
131 to 140 mm		1.14 (26)	1.22 (2)	1.20 (1)	1.14 (29)	136.7	6.3	119.8
141 to 150 mm		1.12 (23)	1.08 (6)	1.22 (2)	1.13 (31)	145.1	6.7	128.6
151 to 160 mm		1.14 (15)	1.12 (22)	1.13 (2)	[2] 1.13 (40)	156.3	7.2	138.3
161 to 170 mm		1.16 (11)	1.14 (36)	1.09 (1)	1.14 (48)	165.5	7.6	144.5
171 to 180 mm		1.18 (1)	1.19 (20)		1.19 (21)	173.9	8.0	146.7
181 to 190 mm			1.15 (8)		1.15 (8)	184.2	8.5	160.2
191 to 200 mm			1.18 (17)	1.14 (4)	1.17 (21)	196.5	8.9	167.6
201 to 210 mm			1.22 (7)	1.35 (1)	1.23 (8)	205.9	9.4	166.9
211 to 220 mm			1.20 (24)	1.22 (10)	1.20 (34)	216.8	9.9	179.9
221 to 230 mm			1.21 (7)	1.20 (6)	1.21 (13)	223.6	10.2	185.2
231 to 240 mm			1.21 (2)	1.08 (1)	1.17 (3)	234.0	10.6	200.7
Average	1.74 (176)	1.25 (218)	1.16 (153)	1.19 (28)	1.24 (576)			

[1] First year of life.
[2] The age was not determined for 1 specimen in this length interval.

These changes in the *L/Sc* ratio perhaps are shown more clearly in table 3 and figure 3. It is evident that the ratio of body length to scale length in the Lake Erie yellow perch is determined primarily by the length of the fish.

Figure 3 is a graphic presentation of the average total lengths and average scale measurements shown in table 3. The straight line extending upward from a fish length of 4.6 inches represents the body-scale relation of all fish with total lengths greater than 4.2 inches, on the assumption that a single average (1.16) describes the body-scale ratio satisfactorily for all these fish. The line for the average fish lengths of 2.3 to 4.6 inches was drawn freehand. The line determined by the average *L/Sc* ratio (1.16) fits the data closely for the fish with average total lengths of 4.6 to 8.9 inches. The scales of those fish with average lengths of 9.4 inches and more were somewhat, but not pronouncedly, smaller than would have

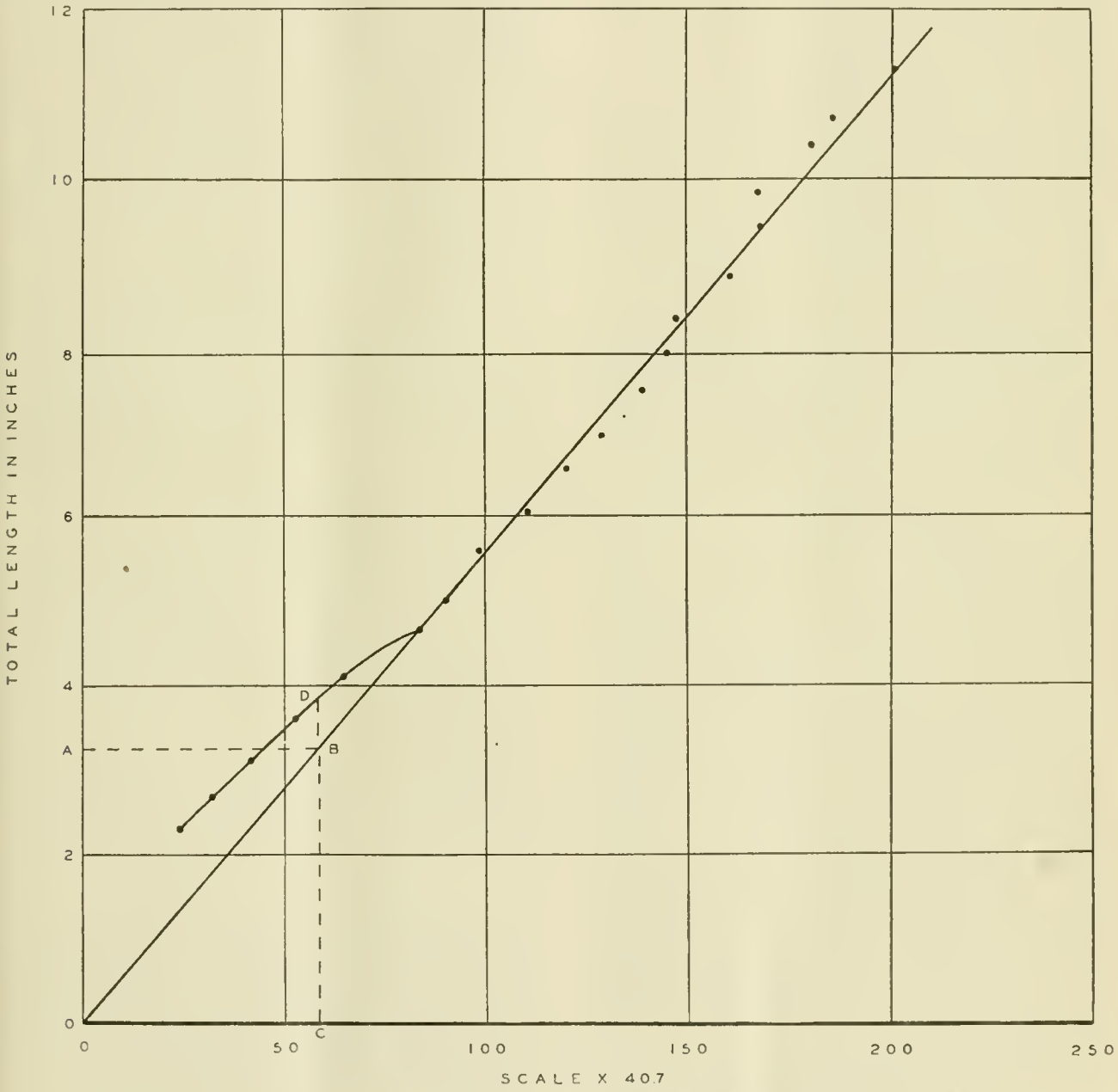

FIGURE 3.—Relation between body length and scale length in yellow perch of Lake Erie.

been expected on theoretical grounds. These rather slight discrepancies which affected only three length intervals are not believed to invalidate the conclusion that the body-scale ratio is constant beyond the average body length of 4.6 inches. The scales from the fish with average lengths of less than 4.6 inches were relatively much smaller than the scales from the larger fish. It is to be noted particularly that the relative size of the scale increased rapidly as the average length of the fish increased from 2.3 to 4.1 inches. The increase in relative size follows approximately a straight line but its slope is greater than that of the line fitted to the data for the larger fish.

The rapid increase in the relative size of the scale during early life was expected from the known facts of scale growth. The scales originate as tiny isolated platelets when the yellow perch has a total length of approximately 1 inch. The scale, then, must grow more rapidly than the body in order to attain the degree of imbrication characteristic of larger fish.

It is evident from table 3 and figure 3 that a sharp break in the series of *L/Sc* values and in the continuity of the curve occurred between the average lengths of 4.1 and 4.6 inches. A detailed examination of the *L/Sc* ratios for each millimeter length indicated that the break occurred at a length of 4.3 inches. The average ratio of the 4.2-inch individuals was comparatively high (1.34), but it fell suddenly to 1.13 in the 4.3-inch fish and continued at that level in the larger specimens. It appears, then, that the *L/Sc* ratio actually assumes constancy at a fish length of 4.3 inches rather than at 4.6 and no corrections for disproportionate growth of body and scale are necessary for calculated values greater than 4.2 inches. Since the two discontinuous portions of the curve of figure 3 were based on averages (in order to obtain a smoother curve) and (for purposes of correcting computed lengths below 4.3 inches) were connected at points of average lengths (4.1 and 4.6), any calculated values that fall between these two averages will be subject to correction. Any correction of length between 4.2 and 4.6 inches theoretically is unwarranted. However, as may be seen from table 4, the corrections for lengths between these limits are small and for all practical purposes may be ignored.

If the length of the scale were purely a function of the length of the fish, the body-scale curve for the smaller individuals would be expected to join smoothly the straight line that describes the body-scale relation for the larger ones. The pronounced discontinuity in the curve suggests that other factors must be involved. Changes in the relative size of the head with increase in fish length may have been a factor. The relative size of the head was found to decrease progressively with increase in fish length through the 71 to 80 mm. interval or up to the average length of 74.6 mm. (3.6 inches total length). Thereafter, variations in the relative size of the head were small and without any detectable trend through the 171 to 180 mm. interval (8.0 inches average total length). Although the progressive decrease in the relative length of the head may have contributed to the decrease in the values of *L/Sc* up to a fish length of 3.8 inches, it is apparent that these changes did not produce the observed sudden shift in the body-scale relation between 4.3 and 4.7 inches.

The possible effect of variations in the number of scales in linear series on the body-scale ratio also was investigated. It was found that fish with standard lengths of 81 to 90 mm. (4.1 inches average total length) averaged 54.9 (51 to 58) scales in the lateral line, and that fish with lengths of 91 to 100 mm. (4.6 inches average total length), averaged 55.1 (51 to 62). The small difference (0.2) in the averages could have had little effect on the changes in the body-scale ratio. If it is assumed that this difference could affect the body-scale ratio, then one would expect the larger fish to have relatively smaller scales, a conclusion contrary to the observed facts. It appears that the number of scales in linear series was not a factor in the sudden change in the body-scale ratio of the Lake Erie yellow perch.

Length of fish is the only factor in these data that can be demonstrated to have had an appreciable effect on the body-scale ratio. The failure of the two portions of the curve to join smoothly cannot be explained satisfactorily as yet.

CALCULATION OF GROWTH

In the preceding discussion it was indicated that because of the discontinuity of the *L/Sc* curve (change in average *L/Sc* ratios) all direct-proportion computations of length less than 4.6 inches must undergo correction, and because of the constancy in the average ratios no corrections were needed for lengths of 4.6 inches or more. The

direct-proportion method was therefore employed whenever the calculated lengths exceeded 4.5 inches and the empirical curve was used only for the smaller lengths. Since the correction for 4.51 inches was less than 0.05 inch, the empirical-curve method was applied only to lengths of 4.46 inches and less.

In practice, all lengths were computed by direct proportion, and corrected lengths corresponding to calculated lengths 4.46 inches and less were read directly from table 4, which was prepared with the assistance of the empirical body-scale curve (fig. 3). The data for this curve were plotted originally on 1-mm. cross-section paper and the amount of each correction was read directly from this graph. The amount of correction required for each direct-proportion calculated length is the vertical distance between the extended straight line representing the body-scale ratio of fish with total lengths of 4.6 inches and more and the empirical line representing the ratio for the shorter fish. The procedure for obtaining the correction for a direct-proportion calculated length of 3.25 inches is illustrated in figure 3. Line AB is drawn horizontally from $L=3.25$ to B on the straight line representing the body-scale ratio of fish with total lengths of 4.6 inches and more. Line CD is a perpendicular that passes through B from the scale axis to D on the line representing the body-scale ratio of the smaller fish. The correction is the distance between points B and D. In the present study only the first-year lengths fell within the range that required correction.

TABLE 4.—*Calculated lengths (inches) of Lake Erie yellow perch*

[Total-length conversion of standard length in millimeters]

Direct-proportion calculated length	Corrected calculated length	Direct-proportion calculated length	Corrected calculated length
1.72	2.63	3.15	3.73
1.77	2.63	3.20	3.78
1.82	2.68	3.25	3.82
1.86	2.72	3.30	3.82
1.91	2.77	3.35	3.82
1.96	2.82	3.39	3.85
2.01	2.87	3.44	3.85
2.06	2.87	3.49	3.90
2.10	2.92	3.54	3.95
2.15	2.96	3.58	3.95
2.20	3.01	3.63	4.00
2.25	3.06	3.68	4.04
2.29	3.11	3.73	4.04
2.34	3.15	3.78	4.09
2.39	3.15	3.82	4.09
2.44	3.20	3.84	4.14
2.49	3.25	3.87	4.14
2.53	3.30	3.90	4.18
2.58	3.30	3.95	4.18
2.62	3.35	4.00	4.23
2.68	3.39	4.04	4.28
2.72	3.39	4.09	4.28
2.77	3.44	4.14	4.28
2.82	3.49	4.18	4.32
2.87	3.54	4.23	4.32
2.92	3.54	4.28	4.37
2.96	3.59	4.32	4.42
3.01	3.63	4.37	4.42
3.06	3.68	4.42	4.46
3.11	3.68	4.46	4.51

CALCULATED GROWTH HISTORIES OF THE AGE GROUPS

The average weight at capture and the calculated lengths of yellow perch taken from impounding nets in the years 1927–37 are shown by sex and age group in table 5. Combination of the data for the several years was possible because the corresponding averages varied but little from year to year and the trends in discrepancies between lengths computed from fish of different ages were the same in each of the year classes. The more rapid growth of the females in all years of life except the second was evident for each year as well as for the combined years.

The corrected calculated lengths at the end of the first year of life are seen to be 0.6 inch greater than those obtained by direct proportion for all age groups of both sexes except group I where the difference was 0.4. The smaller amount of correction for age-group-I fish is to be expected since they were the larger individuals of their year class and hence their body-scale ratio deviated less from the straight-line relation required for direct-proportion computations. In general, the same remarks may be made regarding the data for males, females, and all fish. Without exception the calculated first-year lengths of age-group-I fish were greater than those computed from older fish. The calculated lengths of fish older than age group I revealed a slight tendency for the first-year length to decrease as the fish became older. The discrepancies between the calculated first-year lengths of fish older than group I were small. Comparisons of the calculated lengths for all years of life after the first revealed not only that there was a definite tendency for the lengths to decrease as the fish became older but also that the discrepancies each year were larger than in the first year of life. It is to be noted also that, with the exception of group-II fish, the length at capture in the late fall was greater than the corresponding lengths computed from older fish.

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TABLE 5.—*Average weights and calculated lengths of Lake Erie yellow perch taken in impounding nets in late fall, 1927-37 combined*

[Number of specimens in parentheses]

Age group	Average weight at capture (ounces)	Calculated length [1] (inches) at end of year—					
		1		2	3	4	5	6
		Uncorrected	Corrected					
Male:								
Age group I	3.15	3.6 (266)	4.0 (266)	[2] 7.5 (266)				
Age group II	4.25	3.0 (532)	3.6 (532)	6.7 (532)	8.4 (394)			
Age group III	5.54	3.1 (397)	3.7 (397)	6.5 (397)	8.4 (397)	9.3 (209)		
Age group IV	6.15	2.9 (45)	3.5 (45)	5.7 (45)	7.7 (45)	8.9 (45)	9.6 (23)	
Average [3]		3.0 (974)	3.6 (974)	6.6 (974)	8.4 (836)	9.4 (254)	10.1 (23)	
Annual increment		3.0	3.6	3.0	1.8	1.0	.7	
Female:								
Age group I	2.96	3.5 (37)	3.9 (37)	7.2 (36)				
Age group II	4.66	3.1 (490)	3.7 (490)	6.9 (490)	8.7 (310)			
Age group III	6.57	3.2 (355)	3.8 (355)	6.7 (355)	8.7 (355)	9.9 (192)		
Age group IV	7.40	2.9 (55)	3.5 (55)	5.9 (55)	7.9 (55)	9.3 (55)	10.2 (28)	
Age group V	8.50	2.9 (5)	3.5 (5)	6.0 (5)	7.9 (5)	9.1 (5)	10.0 (5)	10.6 (4)
Average [3]		3.1 (905)	3.7 (905)	6.7 (905)	8.6 (725)	9.8 (252)	10.7 (33)	11.3 (4)
Annual increment		3.1	3.7	3.0	1.9	1.2	.9	.6
All fish: [4]								
Age group I	3.02	3.6 (392)	4.0 (392)	7.4 (371)				
Age group II	4.38	3.1 (1,636)	3.7 (1,636)	6.8 (1,636)	8.5 (750)			
Age group III	5.99	3.0 (895)	3.6 (895)	6.6 (895)	8.5 (895)	9.5 (409)		
Age group IV	6.86	2.8 (108)	3.5 (108)	5.8 (108)	7.9 (108)	9.1 (108)	10.0 (51)	
Age group V	8.50	2.9 (5)	3.5 (5)	6.0 (5)	7.9 (5)	9.1 (5)	10.0 (5)	10.6 (4)
Average [3]		3.1 (2,644)	3.7 (2,644)	6.7 (2,644)	8.5 (1,758)	9.5 (522)	10.4 (56)	11.0 (4)
Annual increment		3.1	3.7	3.0	1.8	1.0	.9	.6

[1] The calculated lengths are based on all fish without regard for time of capture and usually include more specimens than used to determine the length at capture.

[2] The last length shown for each age group is the length at capture late in the fall.

[3] Age group I is not included because of selected size. Beyond the third year of life the average lengths were determined by successive addition of the average annual increments of the age groups for those years.

[4] Includes fish for which the sex was not determined.

In fish older than age group I the discrepancies just described differ from "Lee's phenomenon of apparent decrease in growth rate," as most commonly encountered, in that the wider disagreements occurred among the computed lengths for the later rather than the earlier years of life. It seems probable that the factors that produced the discrepancies in calculated lengths of the Lake Erie perch began to be effective after the first year of life had been passed.

Since an intensive study of the body-scale relation of the Lake Erie yellow perch has eliminated the possibility of large errors in computed lengths resulting from the method of calculation, the observed discrepancies in the calculated lengths must be considered real rather than apparent. In other words, the older fish in the samples actually grew more slowly than the younger ones. The demonstration that the discrepancies in computed growth were real, however, does not justify the conclusion that the data are exactly descriptive of the growth in the population from which the samples were taken. Consideration must be given to the possibility that the samples were not representative of the population as a whole.

DISCREPANCIES IN THE CALCULATED GROWTH HISTORIES OF DIFFERENT AGE GROUPS

Two explanations of the discrepancies in computed growth can be offered. It may be held that the samples were not representative of the population in the lake, and that data based on fully adequate material would not have shown a decline in the growth rate with an increase in age. Or it may be held that the samples were satisfactorily representative but that certain factors tended to bring about the gradual elimination of the more rapidly growing individuals from the yellow-perch population, and that the recorded data therefore represent a valid description of the growth of the Lake Erie perch.

SELECTION BY GEAR

The selective action of impounding nets in taking samples depends on the escape of small fish through the meshes. A rough approximation of the maximum size of escape may be obtained by deter-

mining the length of fish with a girth equal to the circumference of the largest meshes found in the lifting pot of the nets. Since the largest meshes of the impounding nets from which the yellow-perch samples were taken were approximately 2½ inches (stretched measure), no fish with a girth in excess of about 5 inches should be expected to escape from the net. Forty-two perch with an average girth of 5 inches (range, 4.72 to 5.28 inches) had an average total length of 7.9 inches.

Examination of the length-frequency distributions of the age groups (table 19) shows that only the larger of group I were retained because they were too large to escape. About one-fourth of the yellow perch in age group II were as short as the theoretical maximum size of escape; only a few of the group-III fish and none in age groups IV and V were shorter than 7.9 inches.

It is not possible to make precise estimates of the extent to which the reliability of the samples of the different age groups was affected by the selective action of the gear. However, group-I samples were unquestionably composed of individuals with the most rapid growth. Group-II samples were affected much less severely. Beyond age group II, gear selection probably had no significant effect on the reliability of the samples. It may be concluded, then, that inadequate sampling traceable to gear selectivity was an important factor in the discrepancies between the lengths calculated from group-I yellow perch and from older fish, and was a contributing factor in discrepancies between the lengths calculated from group II and from older fish. Discrepancies among age groups older than group II cannot be attributed to the selective action of the nets.

The selective action of the impounding nets serves also as the basis for the differential destruction, correlated with growth rate, that brings about an exaggeration of the discrepancies between the calculated growth histories of yellow perch of different ages. Capture in a commercial net exposes illegal-sized perch [4] to a serious risk of destruction in the fishery since a significant proportion [5] of the undersized yellow perch are dead when the nets are lifted. With a fishery as intensive as that in Lake Erie a single individual may be exposed to destruction repeatedly. Consequently, a severe mortality of the faster-growing yellow perch of the younger age groups, especially age group I, is certain to occur. It appears, then, that perch of the same year class captured at older ages show relatively slow growth not only because the samples of the younger age groups were composed of the faster-growing fish but also because some of these same fast growers were eliminated from the stock as young fish.

SEGREGATION CORRELATED WITH SEXUAL MATURITY

Any segregation of the yellow-perch population according to maturity would be in effect a segregation according to size also, since the proportion of mature individuals increased rapidly with increase in length (table 36), and it was the larger fish in the younger age groups that were mature. It will be shown later that the only evidence of a segregation of yellow perch according to maturity was found during the spawning season when the samples consisted almost entirely of mature fish—97 percent of the yellow perch in samples taken April 11 and 13, 1932, were mature.

A comparison of the percentage of mature individuals at different lengths (table 36) with the length-frequency distribution of the age groups (table 19) provides an indication of the extent to which segregation on the basis of maturity may affect the samples of each age. It is seen in table 36 that a majority of the males reached maturity at 6½ inches but that most of the females were not mature until they had passed 8½ inches. It is apparent from table 19 that of the males only group I would be affected by a segregation on the basis of maturity. Such segregation, however, would practically eliminate the group-I females, seriously affect those in age group II, and to a lesser degree disturb age group III. Because the data in tables 19 and 36 were largely from fish taken in the fall, the remarks concerning each age group may be expected to apply equally well to the next-older group in the next spawning season, since little if any intervening growth would occur. Thus, in the spawning season a segregation on the basis of sexual maturity would affect some of the males and practically all of the females in group II, a few of the males and many of the females in group III, and almost none of the fish in group IV and

[4] Since the legal size for yellow perch (8½ inches total length) is well above the maximum length of escape, the question of differential destruction dependent on gear selectivity concerns only the undersized fish.

[5] Dr. John Van Oosten, U. S. Fish and Wildlife Service, found that approximately 14 percent of the undersized yellow perch were dead in Lake Erie trap nets at the time of lifting.

older groups. The April 11 and 13, 1932, samples seem to bear out this expectation as there were no females in age group II but they accounted for 14.3 and 39.4 percent, respectively, of all fish in age groups III and IV. Although other factors no doubt affected the sex ratio in the April 1932 samples (see section on sex ratio, p. 260), segregation on the basis of maturity must have played an important part.

Inadequate sampling because of segregation according to maturity is of little importance in the present study since only one collection employed in the study of age and growth was taken from the spawning run (1932 collection). In this material the reliability of the data for the group-III females only is open to question.

Since maturity and length are closely related, it is possible that segregation according to maturity may be a source of destruction in the spawning-run fishery of fish with more rapid growth. The effects of this higher mortality of fish with rapid growth on comparisons of the growth histories of fish of different ages are similar to the effects of the selective destruction of rapidly growing fish associated with gear selectivity (p. 221).

SELECTIVE DESTRUCTION ACCORDING TO THE LEGAL SIZE LIMIT

The imposition of a minimum legal size limit does much to reduce the effect of selection by gear through the protection of the faster-growing but still illegal-sized individuals, but at the same time adherence to a legal size limit produces a similar selective effect of its own. As the fish reach the minimum legal size limit they are subject to removal by the commercial fishery. Consequently, the faster-growing individuals are exposed to this source of destruction earlier in life than are those of slower growth. In a heavily exploited fishery, successive samples of a year class, then, may be composed of fish with successively slower growth as a consequence of continued sorting according to size.

The manner and extent to which the selective destruction of yellow perch according to legal size limit may give rise to discrepancies between the calculated growth histories of different age groups are brought out by the data of table 6. Effects of the elimination of different percentages of legal-sized fish [6] on the determination of the growth histories of three age groups also are shown. From the data of table 6 it is obvious that the continued removal of legal-sized yellow perch in the commercial fishery will bring about a decrease in the calculated growth rates of an age group. The first-year computed lengths were affected the least. The exclusion of all legal-sized fish reduced the first-year length by only 0.1 inch in the 1928 group II and 0.2 inch in the 1929 group II but brought about a 0.2-inch increase in the first-year length of the 1928 group III. On the other hand, the effect of the elimination of legal-sized yellow perch on the determination of the calculated lengths at the end of the second and third years of life was pronounced. The decreases in the second-year length with all legal-sized fish excluded were as high as 0.7 inch (1929 group II); the decreases in the third-year length were as high as 0.9 inch (1928 group III). When lesser percentages of

[6] A size limit of 8½ inches was employed in the separation of legal and undersized fish in all three age groups although a 9-inch limit was actually in effect in 1928. Since most of the 1928 samples were taken in the summer before completion of the season's growth and most of the 1929 samples were taken in the fall, presumably after completion of the season's growth, it was believed that the data for all age groups would be made more nearly comparable by the use of a single size limit.

TABLE 6.—*Effect of excluding legal-sized fish in determining growth histories of Lake Erie yellow perch*

[Legal size: 8½ inches]

Proportion of legal-sized fish excluded	1928 group II			1929 group II				1928 group III			
	Number of specimens	Calculated length at end of year of life—		Number of specimens	Calculated length at end of year of life—			Number of specimens	Calculated length at end of year of life—		
		1	2		1	2	3 [1]		1	2	3
None	832	3.8	7.1	372	3.5	6.8	8.5	70	3.7	6.2	8.2
25 percent	750	3.8	7.0	323	3.5	6.7	8.4	57	3.7	6.2	8.1
50 percent	669	3.8	7.0	274	3.5	6.6	8.3	44	3.8	6.1	8.0
75 percent	588	3.7	6.9	225	3.4	6.4	8.1	31	3.8	6.1	7.9
100 percent	506	3.7	6.7	176	3.3	6.1	7.9	18	3.9	5.8	7.3

[1] Length at capture in fall (see footnote 6, above).

legal-sized fish were excluded the reductions in the calculated lengths were smaller.

It should be mentioned that the data of table 6 are based on the elimination of legal-sized fish in a single group of samples whereas the removal of legal-sized individuals by the fishery is gradual and is also progressive in the sense that continued growth during the fishing season brings more and more individuals to the legal size. The data serve, nevertheless, to illustrate the type of selective destruction that must occur in the heavily exploited yellow-perch fishery.

Comparisons of the growth data of table 6 with those of table 5, reveal that the discrepancies produced by the elimination of legal-sized fish from an age group resembled closely the discrepancies that actually occurred between the growth histories of different age groups. It is particularly striking that in both table 6 and table 5, the greatest disagreements among the calculated lengths of fish older than age group I occurred beyond the first year of life. It must be considered probable that selective destruction based on sorting according to the legal size limit was an important contributing factor in the observed discrepancies in the calculated lengths of the different age groups of Lake Erie yellow perch.

OTHER CAUSES

Differential natural mortality connected with rate of growth.—The widely observed association of slower growth with the attainment of greater age in poikilothermic animals which was also found by Hile (1936) in the ciscoes of Silver Lake, Wis., may have been a possible factor in the discrepancies in the calculated growth histories of the Lake Erie yellow perch. The effects of such a differential natural mortality among the Lake Erie perch, however, would be obscured by the more important sources of differential destruction by the fishery.

Annual fluctuations in growth rate.—The discrepancies in calculated growth cannot be traced to annual differences in growth rate since the disagreements occurred between different age groups of the same year class.

Formation of more than one annulus per year.—The validity of the use of the annulus on the Lake Erie yellow-perch scale as a true year mark has been established. Although accessory checks are not infrequent, the scales of those fish concerning whose age there was doubt were discarded. It does not appear reasonable, therefore, to assume that the number of errors in the determination of age was sufficiently great to account for the observed discrepancies in the calculated growth of different age groups.

Contraction and resorption of the scale.—Van Oosten (1929) pointed out that the nature of the structure of scales makes wholly unacceptable the assumption that a contraction of scales occurs. The examination of thousands of yellow-perch scales failed to yield any indication of resorption that would effect the calculation of growth. The limited amount of resorption or erosion observed in the lateral fields of the scales of some old fish did not affect the measurements along the anteroposterior axis of the scales.

GENERAL GROWTH CURVES

GROWTH IN LENGTH

It is not possible to determine a growth curve for the Lake Erie yellow perch that is general in the sense that it describes the growth of an individual typical of the population as a whole. The preceding discussions have brought out clearly that in general the older fish had a slower rate of growth than the younger. Consequently, the combination of the data of several age groups to determine a general growth curve involves the lumping together of heterogeneous growth material. The resulting curve is descriptive of the samples rather than of a typical individual. These limitations to the significance of the data should be kept in mind in the examination of the information on general growth contained in table 7.

The average lengths listed in table 7 have been taken from table 5 and are based on the combination of all age groups except group I, which was omitted as nonrepresentative by reason of gear selection (see p. 221). The lengths of fish taken in the fall (presumably at the end of the growing season) were combined with the corresponding calculated lengths. Beyond the third year of life the average lengths of the different age groups were determined by successive additions of the average annual increments of growth. This procedure brings about a natural smoothing of the general growth curve for the later years of life.

TABLE 7.—*Average calculated length, by age, of Lake Erie yellow perch taken by impounding nets*

Year of life	Number of specimens	Total length	Increment in length	Increase	Standard length
		Inches	*Inches*	*Percent*	*Millimeters*
Males:					
1 year	974	3.6	3.6		76
2 year	974	6.6	3.0	83.3	143
3 year	836	8.4	1.8	27.3	181
4 year	254	9.4	1.0	11.9	203
5 year	23	10.1	.7	7.4	220
6 year					
Females:					
1 year	905	3.7	3.7		77
2 year	905	6.7	3.0	81.1	146
3 year	725	8.6	1.9	28.4	187
4 year	252	9.8	1 2	14.0	215
5 year	33	10.7	.9	9.2	234
6 year	4	11.3	.6	5.6	248
All fish:					
1 year	2,644	3.7	3.7		77
2 year	2,644	6.7	3.0	81.1	146
3 year	1,758	8.5	1.8	26.9	184
4 year	522	9.5	1.0	11.8	208
5 year	56	10.4	.9	9.5	228
6 year	4	11.0	.6	5.8	242

The use of the average annual increments caused the lengths of the fish in the later years of life to be higher than the corresponding average calculated lengths as determined from the individual age groups (table 5). For example, as derived from the general growth curve, the length of the females at the end of the fifth year was 10.7 inches as compared to the values of 10.2 (length at time of capture in the autumn) and 10 inches as determined from age-groups IV and V, respectively. Similarly, this length was 10.1 inches as derived from the growth curve of the males but was only 9.6 inches at time of capture in the autumn. Discrepancies occurred also in the lengths at the end of the fourth and sixth years of life. Although the successive additions of the average annual growth increments, to determine the general growth curve in the later years, introduce discrepancies, they cannot be held with certainty to represent errors in the general growth curve. On the contrary, the use of the average annual increments may tend to offset the distorting effects of the differential destruction of the more rapidly growing individuals; hence the seemingly greater lengths of the general growth curve may approximate the true typical growth of the Lake Erie yellow perch more closely than a curve based entirely on grand-average calculated lengths.

Figure 4 is a graphic presentation of the data of table 7 on length at the end of each year of life and the annual growth increment. At the end of the first year of life the females were slightly larger (0.1 inch) than the males, and they maintained this advantage in length during the second year. Beginning in the third year the females increased in length progressively faster than males of the same age until at the end of the fifth year they were 0.6 inch longer.

Of particular interest is the fact that the minimum legal size of 8½ inches, effective in the States of Michigan and Ohio, was reached at the end of the third year by all fish (sexes combined). It may be seen also (table 5) that the average length of the males captured late in the fall at the end of their third year was only slightly less (8.4 inches) and that of the females only a little more (8.7 inches) than the legal minimum. The maximum length of yellow perch examined in Lake Erie was 13.9 inches total length, sex not determined. The longest male was 11.3 inches and the longest female 12.9.

No physiological explanation can be offered for the difference in the growth of the sexes. It is rather certain, however, that the earlier attainment of sexual maturity by the males was not the primary cause of their poorer growth. The females enjoyed the greatest actual and relative advantage in growth in the fourth year of life (females 1.2 inches, males 1 inch). Yet at that size 86.1 percent of the females and 98.6 percent of the males were mature (see table 36). If the poor growth of the males was the result of their early attainment of maturity, the greatest advantage in the growth of the females would be expected to occur in the second year of life when 57.8 percent of the males and none of the females were mature.

In spite of the differences in the growth of the sexes, the same general description of the course of growth applies to the curves for the females, males, and the sexes combined. The most rapid growth in length took place in the first year of life, after which the annual increments decreased continuously.

GROWTH IN WEIGHT

The average weights of the age groups of yellow perch taken late each fall (table 5) bring out clearly that the females were heavier at each age than the males with the exception of those fish assigned to age group II in which the males also were the longer. The best-represented age group (II), which characteristically dominates the late-season

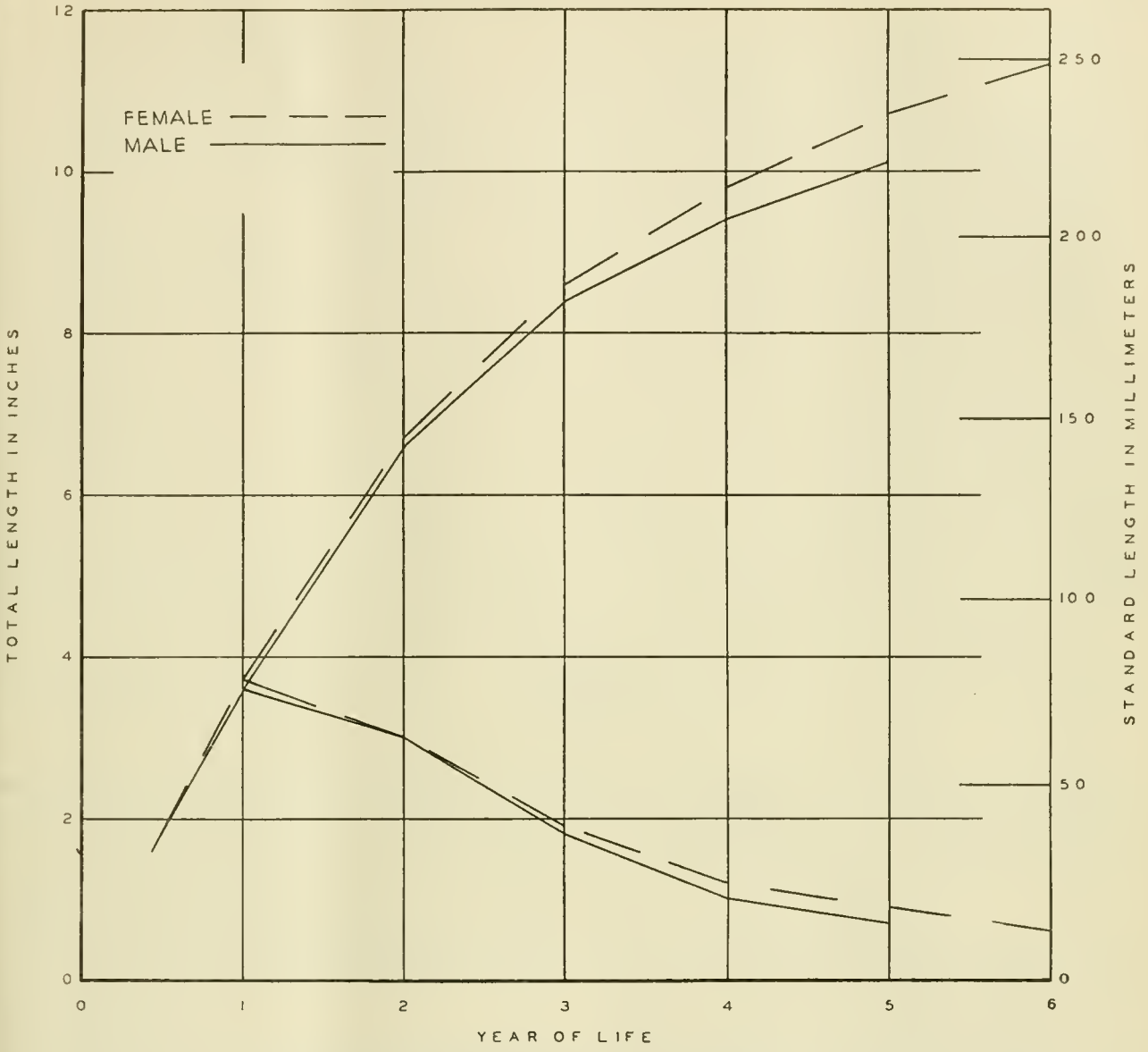

FIGURE 4.—General growth curves showing average length and average annual increments in length of Lake Erie yellow perch at end of each year of life.

catches by trap nets, had an average weight of just over 4 ounces. The only group with an average weight of over 8 ounces (V) was represented by only four fish in the late fall samples and, therefore, the reliability of the average is open to question. Although there was considerable annual variation, the values in table 5 are believed to represent rather well the average weights of yellow perch taken by trap nets from Lake Erie during the later season.

The average weights of the age groups captured late in the autumn differed considerably from the corresponding calculated weights (tables 5 and 8). The empirical weights were greater for the younger fish and smaller for the older individuals. Net selectivity, whereby only the heavier of the shorter fish were retained, no doubt accounted for the greater empirical weights of the younger fish. Perhaps the decrease in condition during October and November (p. 255) was enough to bring about the discrepancies noted among the older ages.

In order to have strictly comparable data for general growth in length and in weight, the equation for the length-weight relation of the Lake

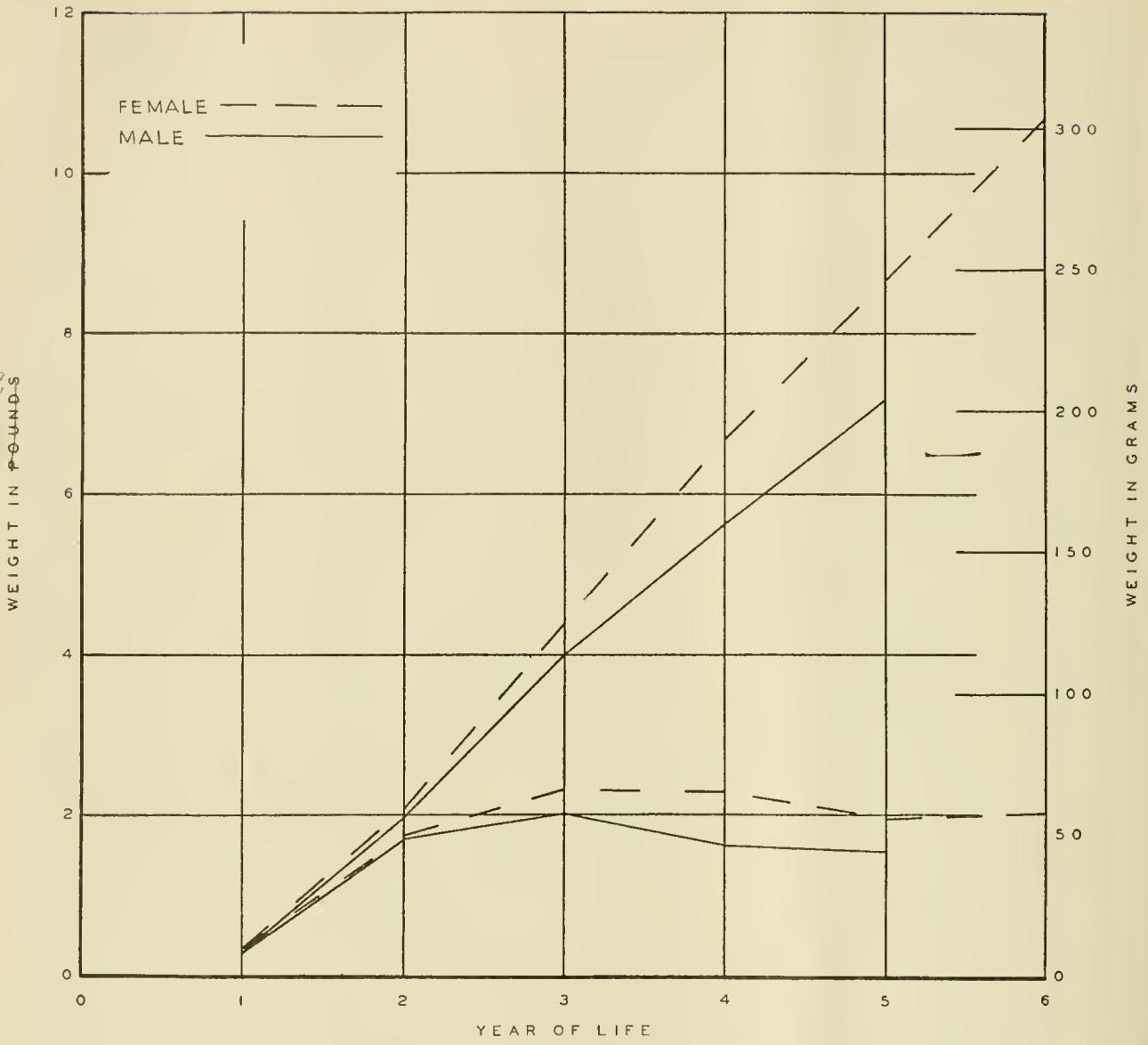

FIGURE 5.—General growth curves showing average calculated weight at end of each year of life and average annual increase in weight of Lake Erie yellow perch according to sex.

TABLE 8.—*Average calculated weight, by age, of Lake Erie yellow perch*

[Collections of all years combined]

Year of life	Weight		Increment in weight	Increase
	Grams	Ounces		
			Ounces	*Percent*
Males:				
1 year	8	0.28	0.28	
2 years	56	1.98	1.70	607.1
3 year	113	3.99	2.01	101.5
4 year	160	5.64	1.65	41.4
5 year	204	7.20	1.56	27.7
6 year				
Females:				
1 year	9	.32	.32	
2 year	59	2.08	1.76	550.0
3 year	125	4.41	2.33	112.0
4 year	190	6.70	2.29	51.9
5 year	246	8.68	1.98	29.6
6 year	303	10.69	2.01	23.2
All fish:				
1 year	9	.32	.32	
2 year	58	2.05	1.73	540.6
3 year	119	4.20	2.15	104.9
4 year	172	6.07	1.87	44.5
5 year	224	7.90	1.83	30.1
6 year	279	9.84	1.94	24.6

Erie perch (see p. 252) has been employed to compute weights corresponding to the grand-average lengths of table 7. These calculated weights are given in table 8 which shows also the annual increments and percents of increase in weight. The data on general growth in weight are presented graphically in figure 5.

The calculated weights of the females exceeded those of the males in every year of life. The advantage of the females increased regularly from 0.04 ounce at the end of the first year of life to 1.48 ounces at the end of the fifth. The greatest advantage in the growth of the females occurred in the fourth year of life when the increment was 2.29 ounces as compared to 1.65 for the males.

For each sex and for the sexes combined the annual percent increase in weight was greatest in the second year and decreased continuously in the later years. The greatest actual increase in weight occurred in the third year of life. At the end of the third year, when the Lake Erie yellow perch attained the legal length, 8½ inches, the weight (4.2 ounces) was less than half that at the end of the sixth year (9.8 ounces). The heaviest male weighed 12¼ ounces and the heaviest female (a gravid specimen) weighed 19¾ ounces.

GROWTH OF YELLOW PERCH IN LAKE ERIE COMPARED WITH THAT IN OTHER WATERS

Comparison of the growth of yellow perch in Lake Erie with that in other waters will be based on data from the major centers of commercial production of the species. With reference to other waters, it is sufficient to say that the numerous published average lengths of the age groups show tremendous variation in the size of fish of the same age. There appears to be no correlation between geographical location of the lakes and the rate of growth of perch.

Table 9 gives the average calculated total length of yellow perch at the end of each year of life as determined in the present study;[7] by Hile and Jobes for Saginaw Bay (1941) and for the Wisconsin waters of Green Bay and northwestern Lake Michigan (1942); and by Carlander (1942) for the Minnesota waters of Lake of the Woods. The data are presented graphically in figure 6. The total lengths shown were determined where necessary from standard lengths in millimeters by use of the appropriate conversion factors. Calculated lengths at the end of each year of life are used rather than length of the age groups at capture to eliminate discrepancies caused by differences in the time of capture.

With the single exception of the first year when the growth from Lake of the Woods was the greatest (3.9 inches), the yellow perch were larger in Lake Erie and Saginaw Bay than in the other three areas. The Lake Erie yellow perch were larger than those from Saginaw Bay in the first 3 years of life. In the fourth year they averaged the same, but thereafter the Saginaw Bay

TABLE 9.—*Comparison of average calculated total lengths of yellow perch from several localities*

[Data for sexes combined]

Locality	Average calculated length (in inches) at end of year—										
	1	2	3	4	5	6	7	8	9	10	11
Lake Erie	3.7	6.7	8.5	9.5	10.4	11.0					
Saginaw Bay	3.0	5.3	8.0	9.5	10.7	12.0	12.8				
Green Bay	2.8	4.6	6.3	7.9	9.0	10.2	11.2	12.3	13.9		
Northwestern Lake Michigan	2.8	4.5	6.0	7.1	8.5	9.7					
Lake of the Woods	3.9	5.4	6.9	8.1	9.2	10.5	11.8	12.9	14.1	15.2	16.6

[7] Data on the Lake Erie yellow perch published by Harkness (1922) are not included in the table because of differences in criteria for recognizing annuli, and his estimated lengths were not computed with reference to the end of years of life. Study of these scales, which he kindly sent to me, failed to reveal any pronounced differences in the rates of growth of yellow perch collected by him in 1920 and of those collected in 1927 and used in the present study.

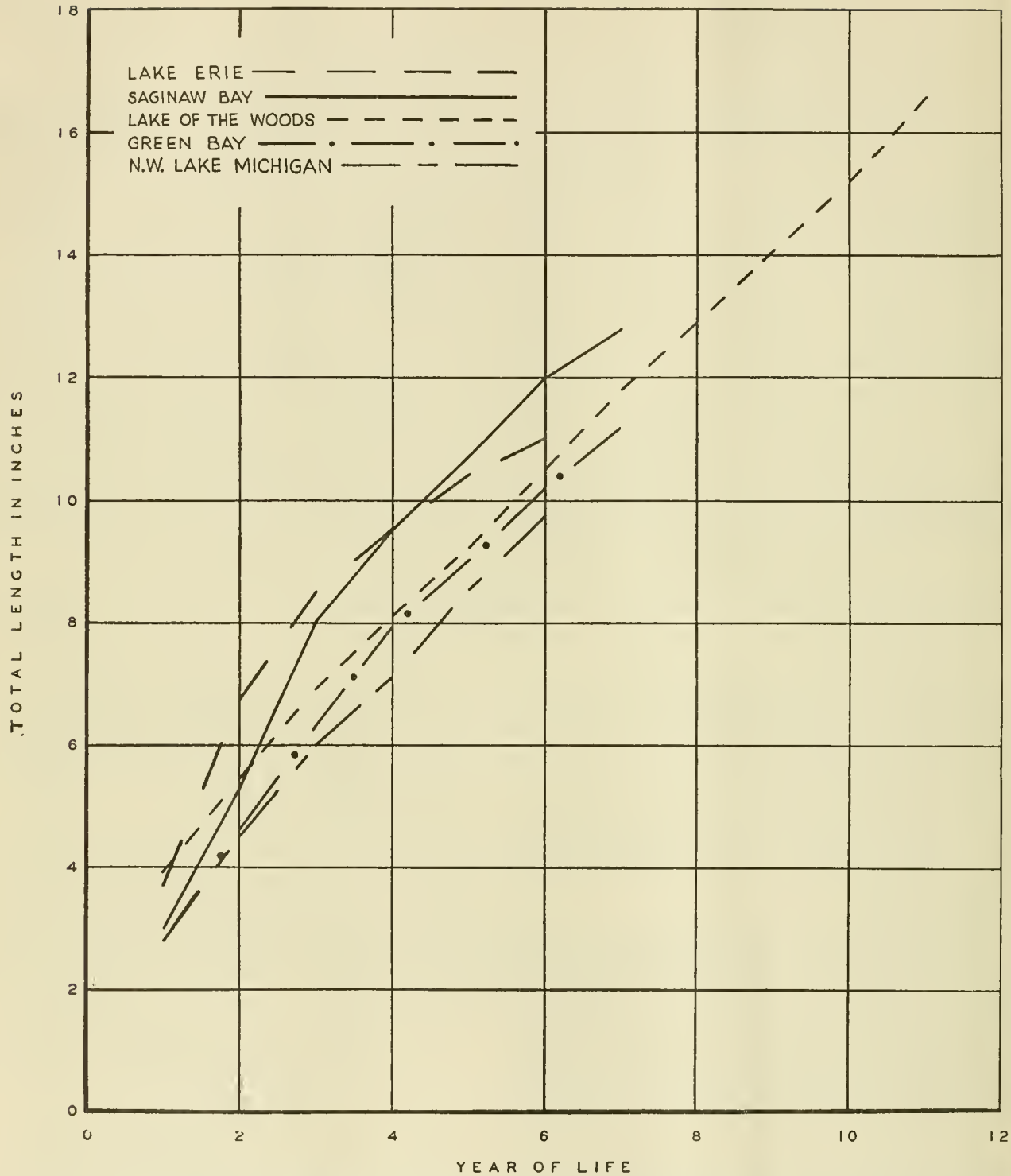

FIGURE 6.—Average calculated total length in inches at end of each year of life of yellow perch from different waters of the Great Lakes and Lake of the Woods. Sexes combined.

fish averaged the larger. There is a striking similarity in the growth curves of the other three populations (fig. 6). The yellow perch from Lake of the Woods averaged about 1 inch longer than those from Green Bay and northwestern Lake Michigan at the end of the first year, and after this year the individuals from northwestern Lake Michigan averaged somewhat shorter than those from the other two areas.

Although each of these growth rates compares favorably with those from other waters, slow growth does occur in the Great Lakes. Van Oosten (1944) reported a sample of yellow perch taken from Presque Isle Bay (Lake Erie) that averaged only 6.7 inches total length as age-group-IV fish. Apparently these slow-growing fish do not frequent Lake Erie proper as none was found among the thousands examined in the course of the present study. The largest yellow perch taken from Lake Ontario by Greeley (1940) had a total length of just more than 6.5 inches in its fifth summer of life.

GROWTH COMPENSATION

Two types of relation between early size and subsequent growth have been observed: (1) That in which the individuals with greater growth in the first year retain or add to that advantage in later growth; and (2) that in which the individuals with greater growth in the first year grow relatively more slowly each subsequent year so that a reduction in range of size occurs. This latter relation is known as growth compensation. No attempt will be made to review the literature on the subject, but it may be stated that the phenomenon of growth compensation has been observed in so many species of fish, both marine and fresh-water, that its occurrence may be considered general.

Age groups II and III of the 1929 collection, both of which contained large numbers of specimens, have been selected for a study of the relation between the first-year length and the later growth in length of the Lake Erie yellow perch. The data have been restricted further to those fish collected late in the autumn, when it could be assumed that the year's growth was complete. Table 10 shows the growth histories of the different yearling-size classes (sexes separately) of each of these age groups.

The first-year difference of 0.99 inch between the average lengths of the largest and smallest group-II males was increased to 1.38 inches in the second year. The maximum difference was reduced by compensatory growth in the third year to 1.05 inches, but nevertheless remained above the original difference. In the group-II females the original 0.94-inch advantage of the largest yearlings over the smallest was increased slightly to 0.97 inch in the second year. The maximum difference was reduced by compensatory growth in the third year to only 0.68 inch.

TABLE 10.—*Relation between calculated length of Lake Erie yellow perch at end of first year and growth in subsequent years, based on 1929 collections of age groups II and III*

Calculated length at end of first year of life	Number of specimens	Length (inches) at end of year—				Increment (inches) for year—			
		1	2	3	4	1	2	3	4
Age group II:									
Males:									
3.35 inches and under	59	3.15	6.24	8.22		3.15	3.09	1.98	
3.36 to 3.82 inches	77	3.58	6.88	8.55		3.58	3.30	1.67	
3.83 inches and over	29	4.14	7.62	9.27		4.14	2.68	1.65	
Maximum difference		.99	1.38	1.05					
Females:									
3.35 inches and under	49	3.15	6.28	8.27		3.15	3.13	1.99	
3.36 to 3.82 inches	64	3.58	6.88	8.63		3.58	3.30	1.75	
3.83 inches and over	27	4.09	7.25	8.95		4.09	3.16	1.70	
Maximum difference		.94	.97	.68					
Age group III:									
Males:									
3.35 inches and under	40	3.11	5.50	7.48	8.86	3.11	2.39	1.98	1.38
3.36 to 3.82 inches	68	3.58	6.42	8.27	9.27	3.58	2.84	1.85	1.00
3.83 inches and over	70	4.09	7.21	8.81	9.73	4.09	3.12	1.60	.92
Maximum difference		.98	1.71	1.33	.87				
Females:									
3.35 inches and under	40	3.20	5.97	7.99	9.46	3.20	2.77	2.02	1.47
3.36 to 3.82 inches	57	3.63	6.38	8.50	9.73	3.63	2.75	2.12	1.23
3.83 inches and over	58	4.18	7.58	9.32	10.33	4.18	3.40	1.74	1.01
Maximum difference		.98	1.61	1.33	.87				

The relation between first-year length and later growth in length of both sexes of age group III resembled that of the group-II males. The largest yearlings of both the males and females added materially to their first-year advantage over the smallest yearlings during the second year of life. The maximum difference was reduced by compensatory growth during the third year, but remained greater than the original difference. In

the fourth year further growth compensation reduced the maximum difference below the first-year value.

It appears to be characteristic of the growth of the Lake Erie yellow perch that a first-year advantage in size is increased in the second year. Growth compeusation occurs in the third and fourth years of life.

PROPORTION OF SEASON'S GROWTH COMPLETED AT TIME OF CAPTURE

TABLE 11.—*Increment of growth completed by Lake Erie yellow perch at certain dates in 1927*

Age group and sex	For fish captured— Oct. 24	Oct. 31 to Nov. 21
Season's growth (increment of standard length) to date of capture:		
Age group I:	*Mm.*	*Mm.*
Males	76	80
All fish [1]	75	79
Age group II:		
Females	46	50
Males	38	47
All fish [1]	39	47
Age group III:		
Females	21	28
Males	27	29
All fish [1]	19	29
Proportion of season's growth completed to date of capture:		
Age group I:	*Percent*	*Percent*
Males	95	100
All fish [1]	95	100
Age group II:		
Females	92	100
Males	81	100
All fish [1]	83	100
Age group III:		
Females	75	100
Males	93	100
All fish [1]	66	100
Average (weighted) percentage	88	100
Specimens:		
Age group I:	*Number*	*Number*
Males	28	136
All fish [1]	40	195
Age group II:		
Females	3	46
Males	15	95
All fish [1]	22	170
Age group III:		
Females	2	15
Males	2	21
All fish [1]	8	39

[1] Includes fish whose sex was not determined.

TABLE 12.—*Increment of growth completed by Lake Erie yellow perch at certain dates in 1928*

Age group and sex	For fish captured— July 17 and 23	Aug. 4 and 8	Aug. 23	Sept. 5	Oct. 16 and Nov. 20
Season's growth (increment of standard length) to date of capture:	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Age group I: All fish [1]			52		74
Age group II:					
Female			26	29	37
Male			20	27	34
All fish [1]	15	18	26	29	37
Age group III:					
Female			20	26	24
Male			20	23	22
All fish [1]	16	21	19	24	24
Proportion of season's growth completed to date of capture:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Age group I: All fish [1]			70		100
Age group II:					
Female			70	78	100
Male			59	79	100
All fish [1]	40	49	70	78	100
Age group III:					
Female			83	108	100
Male			91	104	100
All fish [1]	67	88	79	100	100
Average (weighted) percentage	45	50	71	80	100
Specimens:	*Number*	*Number*	*Number*	*Number*	*Number*
Age group I: All fish [1]			7		4
Age group II:					
Female			104	68	77
Male			40	70	86
All fish [1]	107	151	242	148	184
Age group III:					
Female			2	5	18
Male			3	5	7
All fish [1]	21	5	9	10	25

[1] Includes fish whose sex was not determined.

Although the dates of collection of the Lake Erie yellow perch were not distributed in such a manner as to permit a thoroughgoing study of the progress of growth during the season, scattered data based on samples taken after June 30 do provide a certain amount of information. The calculated increments of growth added in the year of capture and the percentages of these increments of the year's total growth are shown in tables 11, 12, and 13 for three age groups collected in 1927, 1928, and 1929. The growth increments of perch from late-season collections have been considered to represent the total season's growth and hence have been assigned the percentage of 100. The selection of these late-season samples was not arbitrary, but was based on a careful study of the growth increments of fish in the collections of single days. For example, detailed data for 1928 (not given here) demonstrated that the growth increments of perch captured on October 16 were as large as those of fish taken on November 20. It was assumed, therefore, that no growth occurred after October 16 in that year, and consequently the sample of that date was included as part of the "late-season" collection. In 1927, on the other hand, the growth increments of perch captured on October 24 were noticeably smaller than those of fish taken on October 31 and on various dates in November. Accordingly, the October 24 sample was excluded in the computation of the

TABLE 13.—*Increment of growth completed by Lake Erie yellow perch at certain dates in 1929*

Age group and sex	For fish captured— July 1	Aug. 29 and Sept. 5	Sept. 23	Nov. 12 to Dec. 7
Season's growth (increment of standard length) to date of capture:				
Age group I:	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Females			67	64
Males				72
All fish [1]		62	67	70
Age group II:				
Females	9		42	39
Males	8		38	39
All fish [1]	9	41	40	39
Age group III:				
Females	3		26	27
Males	1		21	22
All fish [1]	2	20	24	25
Proportion of season's growth completed to date of capture:				
Age group I:	*Percent*	*Percent*	*Percent*	*Percent*
Females			105	100
Males				100
All fish [1]		89	96	100
Age group II:				
Females	23		108	100
Males	20		97	100
All fish [1]	23	105	102	100
Age group III:				
Females	11		96	100
Males	4		95	100
All fish [1]	8	80	96	100
Average (weighted) percentage	9	90	96	100
Specimens:				
Age group I:	*Number*	*Number*	*Number*	*Number*
Females			1	17
Males				53
All fish [1]		12	1	70
Age group II:				
Females	8		6	140
Males	5		3	168
All fish [1]	13	42	9	308
Age group III:				
Females	96		44	155
Males	35		60	178
All fish [1]	131	64	104	333

[1] Includes fish whose sex was not determined.

full-season increments of growth.[8] Other combinations of collections, as for example, that of the samples of July 17 and 23, 1928, were made only after examination proved the combinations to be warranted.

The data of tables 11, 12, and 13 were presented in considerable detail to bring out the fact that neither sex nor age appeared to affect the course of the season's growth. Females did not show consistently lower or higher percentages than males taken on the same day or days; neither did the percentages vary consistently among samples of different age groups captured on the same dates. It appears valid, therefore, to employ the weighted percentages (given in each table) as measures of the proportion of season's growth completed at different dates.

In order to obtain a more definite idea of the course of growth through the season, the weighted percentages of tables 11, 12, and 13 were plotted as functions of time within the season (fig. 7). The smooth curve appearing in figure 7 was fitted by inspection to the percentages for 1928 and 1929. For reasons to be brought out presently the single percentage available for 1927 (that of growth up to October 24) was held to represent exceptional conditions and was disregarded in the fitting of the curve.

If the curve of figure 7 is accepted as descriptive of the normal course of growth of the yellow perch during the season, the following estimates are obtained:

For month of—	*Percent of total growth end of month*	*Percent of total growth within month*
June	15	15
July	50	35
August	80	30
September	100	20

According to these estimates relatively little growth was completed before July 1 (only 15 percent of the total). The greatest increase in length in a single month occurred in July (35 percent). Growth dropped slightly in August (to 30 percent) and sharply in September (to 20 percent), and appears to have ceased toward the end of September. The small percentage completed on July 1 suggests that growth began some time in June, although it is not possible to be certain on that point.

The preceding description of the course of the growth of the yellow perch during the season must be recognized as merely an approximation since it was based on rather limited and scattered data. The data for 1927 indicate that with exceptional conditions the percentage of total growth completed at different times within the growing season may vary considerably. Perch collected on October 24, 1927, were found to have completed only 88 percent of the estimated total growth for the season. Although the indicated growth of 12 percent of the season's total between October 24 and October 31 does seem to be too high, the data provide evidence, nevertheless, that growth was proceeding actively in October.

[8] Estimates of the progress of growth during the season of capture made by Hile, for the cisco (1936) and for the rock bass (1941) in the lakes of northeastern Wisconsin, were based on comparisons of the growth increments up to the time of capture with the full-season growth as calculated from samples of the same year class in collections of later years. The severe discrepancies between the calculated growth histories of different age groups of the same year class of the Lake Erie yellow perch prohibit the use of the same procedure in the present study.

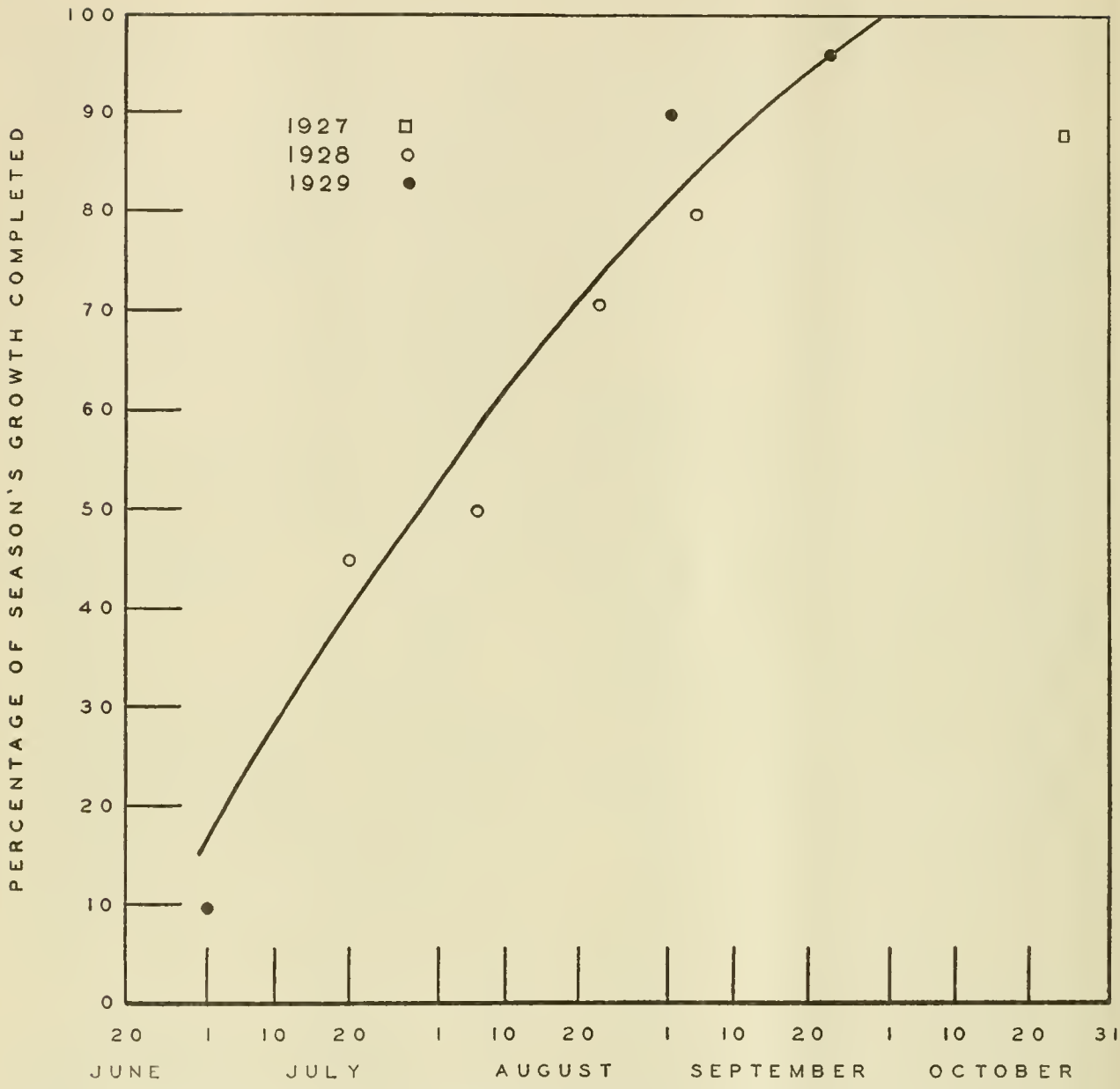

FIGURE 7.—Percentage of season's growth completed at different dates by Lake Erie yellow perch. Curve fitted to 1928–29 data by inspection.

Exceptional conditions may be expected also to affect the course of growth in the early season (earlier onset or more rapid early-season increase in some years).

ANNUAL FLUCTUATIONS IN GROWTH

Data are available for the analysis of fluctuations in the growth of the yellow perch taken by impounding nets in Lake Erie in the two periods, 1927–29 and 1943–48. Although the annual increments of growth in the years 1924–29 were computed from samples of the entire take by the nets, whereas the growth in 1940–48 was determined only from the legal-sized fish (8½ inches and larger), the average annual increments did not differ greatly. The fluctuations in growth were determined separately for each period and represent deviations from the average of the period to

TABLE 14.—*Calculated annual growth increments according to calendar year and year of life of Lake Erie yellow perch taken by impounding net, 1927–29*

[Data for sexes shown separately]

Year of life	Calculated growth increments (inches) in—					
	1924	1925	1926	1927	1928	1929
Males:						
Age group III:						
Fourth year	------	------	------	1.2	0.9	0.9
Third year	------	------	1.9	1.9	1.8	------
Second year	------	2.3	2.6	2.9	------	------
First year	3.6	3.6	3.8	------	------	------
Age group II:						
Third year	------	------	------	2.1	1.4	1.7
Second year	------	------	2.7	3.3	3.2	------
First year	------	3.6	3.8	3.6	------	------
Females:						
Age group III:						
Fourth year	------	------	------	1.2	1.0	0.9
Third year	------	------	1.9	2.3	2.0	------
Second year	------	2.4	2.7	3.0	------	------
First year	3.7	3.5	3.8	------	------	------
Age group II:						
Third year	------	------	------	2.3	1.3	1.7
Second year	------	------	2.9	3.4	3.2	-----
First year	------	3.5	3.8	3.6	------	------

which the individual years belong. The analysis has been confined to the growth of age groups II and III since other age groups contained too few fish to give reliable averages in all years.

The calculated annual increments of age groups II and III taken in 1927–29 are shown for each sex in table 14 and those for the fish taken in 1943–48 are given in table 15. The data in both tables are arranged so that the horizontal rows show the growth in different calendar years of fish in the same year of life. The vertical columns show the growth in a single calendar year of fish in different years of life. The growth histories of the individual age groups are shown in rows running diagonally from the bottom to the right.

The method of estimating annual fluctuations in growth may be illustrated by the 1925 and 1926 data for the females in table 14. The 1926 growths of 2.7, 3.8, and 3.8 inches of age group III in the first and second years of life and of age group II in the first year of life totaled 10.3 inches or 0.9 inch more than the total (9.4) of the corresponding increments in 1925 (2.4, 3.5, and 3.5). The average of the two totals is 9.85 inches. Compared with this average, the total growths in 1926 showed an improvement of 9.1 percent. A continuation of this procedure shows the percentage change in growth from each year to the next. The position of each year's growth with respect to that of 1924 is obtained by the successive addition of the percentages of change. For example, the growth of the group-III females decreased 5.6 percent from 1924 to 1925 as determined by this method of computation, but as indicated above, that of the group-II and group-III females increased 9.1 percent from 1925 to 1926. Hence, the growth in 1926 may be said to have been −5.6+ 9.1, or 3.5 percent better than in 1924. In order to make the percentage deviations describe the changes with respect to average growth over the period 1924–29, rather than only to growth in 1924, the mean of the deviations as computed by the above procedure was subtracted from the individual deviation of each year. The same procedure was used to determine the annual fluctuations in growth in 1940 to 1948 (table 15). The method just described for obtaining the percentage deviations from average growth is that employed by Hile (1941) to determine the annual fluctuations in growth of the Nebish Lake (Wisconsin) rock bass.

TABLE 15.—*Calculated annual growth increments according to calendar year and year of life of Lake Erie yellow perch taken by impounding net, 1943–48*

[Data for sexes combined]

Year of life	Calculated growth increments (inches) in—								
	1940	1941	1942	1943	1944	1945	1946	1947	1948
Age group III:									
Fourth year	-----	-----	-----	1.2	1.3	1.1	1.1	1.3	1.4
Third year	-----	-----	2.1	1.6	1.9	1.6	2.0	1.7	-----
Second year	-----	2.4	2.5	2.8	3.1	2.5	2.4	-----	-----
First year	3.7	3.9	3.6	3.9	3.5	3.8	-----	-----	-----
Age group II:									
Third year	-----	-----	-----	1.8	1.9	1.9	2.1	1.9	2.4
Second year	-----	-----	3.1	3.4	3.3	3.3	3.6	3.0	-----
First year	-----	4.1	3.9	3.7	3.8	3.5	3.8	-----	-----

The annual percentage deviations of the growth of the Lake Erie perch from the 1924–29 and 1940–48 means are shown in table 16 for the sexes separately, where possible, and for the sexes combined. Particularly noteworthy is the very close agreement between the percentage deviations of the sexes. The coefficient of correlation between the annual deviations in the growth of the sexes has the high value of 0.959. This close correlation may be construed as a strong argument for the reliability of the percentages in table 16 as true measures of the annual fluctuations in growth.

The annual variations in the growth of the Lake Erie yellow perch were fairly large. The ranges for the percentages in the period 1924–29 were 23.2 percent for the females, 15.2 percent for the males, and 18.3 percent for the sexes combined. The range in the percentage variation of the sexes

TABLE 16.—*Deviations in growth rate of Lake Erie yellow perch and in mean air temperatures at Sandusky, Ohio, from 1924–29 and 1940–48 averages*

Year	Deviation from average growth			Deviations of mean temperatures					
	Male	Female	Average	May	June	July	August	September	October
	Percent	*Percent*	*Percent*	°F.	°F.	°F.	°F.	°F.	°F.
1924	−4.8	−10.2	−7.5	−3.9	−0.7	−1.9	0.3	−4.5	3.0
1925	−4.8	−4.6	−4.7	−1.6	5.5	−1.1	.6	3.3	−8.3
1926	2.3	4.5	3.4	1.8	−1.5	.0	2.8	.1	−1.4
1927	8.5	13.0	10.8	1.2	−1.9	.2	−4.2	3.3	4.4
1928	−6.7	−7.4	−7.0	2.1	−2.1	2.1	2.8	−2.6	3.6
1929	5.5	4.8	5.2	.6	.5	.6	−2.1	.3	−1.0
1940			−3.1	−2.0	.2	1.1	−.3	−2.5	−.9
1941			2.2	4.4	1.0	1.3	−.9	2.9	2.2
1942			−1.7	3.0	.4	1.1	−.9	−1.3	−.1
1943			−.4	−.4	4.0	.8	.1	−3.3	−2.4
1944			1.8	5.4	2.8	.5	1.5	−.1	−1.5
1945			−4.2	−5.0	−2.8	−2.1	−.1	1.1	−2.3
1946			3.4	−1.0	−1.0	−.7	−4.1	.7	3.5
1947			−7.4	−2.9	−3.2	−2.5	4.7	.8	6.5
1948			9.7	−1.9	−1.4	.6	−.3	1.7	−4.7
Correlation (*r*) between growth and temperature (sexes combined)				.346	−.030	.347	−.605	.504	−.117

combined during the 1940–48 period was 17.1 or a little less than in the 1924–29 period. Growth was below average in 1924 but improved each year until the maximum was reached in 1927. The sharp decline in 1928 was followed by an improvement in 1929. Growth in 1940 was below the average for the period 1940–48. The increase in 1941 was followed by a 3-year period in which the growth fluctuated but little; the variations were greater in 1945–48. The poorest growth in the 1940–48 period was in 1947 and the best in 1948.

Neither a detailed discussion of all the probable factors that contributed to the annual fluctuations observed in the growth of the Lake Erie yellow perch nor a review of the literature on fluctuations in the growth of fish seems desirable. It may be stated, however, that chief among the factors that previous investigators found associated with annual fluctuations in growth rate were changes in the density of the population and fluctuations in weather conditions (temperature and precipitation).[9]

It is not possible to state definitely whether fluctuations in the density of the yellow-perch population affected the growth of the species in Lake Erie. Three years in which growth was above average (1926, 1927, and 1929) and a year of poor growth (1928) occurred when members of the strong year class of 1926 were abundant. This situation suggests that fluctuations in the density of the population may have little or no effect on the growth rate of the Lake Erie perch.

In the study of the relation between meteorological conditions and the growth rate of the Lake Erie yellow perch, detailed records of rainfall, the percentage of possible sunshine, mean wind velocity, and temperature were consulted. Preliminary analyses of the data demonstrated that no correlation existed between growth rate and the first three of the meteorological factors. Seemingly, variations in the amount of sunshine did not affect the production of food sufficiently to influence the growth of the perch. The influence of rainfall which would affect turbidity and the chemical content of the water, and of variation in wind velocity which would affect turbidity, appeared to be too small to detect, or was obscured by other factors.

Investigation of the relation between annual fluctuations in temperature and in the growth rate of the Lake Erie yellow perch yielded suggestive results. The annual deviations of the air temperatures at Sandusky, Ohio,[10] from the 1924–29 and 1940–48 averages in each month from May to October, and the coefficients of correlation between the annual deviations of growth and of temperature in each month are shown in table 16. Included in the table are data not only for the four months, June through September, that were held to constitute the normal growing season (p. 231), but also for May and October. Evidence was brought out that under exceptional conditions growth may continue through October (p. 230), and it is believed possible that temperatures in May can

[9] Hile (1936) and Van Oosten (1944) have reviewed the literature on the causes of fluctuations in the growth rate of fish.

[10] These data on air temperatures were taken from Climatological Data of the United States by Sections, Weather Bureau, U. S. Department of Agriculture.

affect the time at which the season's growth begins. It is recognized that air temperatures do not provide an exact measure of water temperatures, but air temperatures averaging exceptionally high or low over the period of a month probably have a significant effect on the average water temperatures, especially in such shallow water as in western Lake Erie. Doan (1942) concluded that either air or water temperatures may be used to indicate monthly variations from normal, as the two fluctuate similarly.

Of the six coefficients of correlation between annual fluctuations in growth rate and in the air temperatures of individual months listed in table 16, only that for August ($r=-0.605$) may be termed "significant" ($r=\pm 0.514$ when $p=0.05$). The coefficient for September ($r=0.504$) fell just short of the significant value and those for July ($r=0.347$) and May ($r=0.346$), though moderately high were far from significant. The extremely low values for October ($r=-0.117$) and June ($r=-0.030$) offer not the slightest suggestion of any correlation between annual fluctuations in growth rate and temperatures in those months.

Even if temperature were known to be a major factor in the determination of annual fluctuations in growth rate, high correlations between growth and temperature in individual months could hardly be anticipated, since, as has been demonstrated previously, the growing season of the Lake Erie perch includes all or part of several months. It was with this in mind that the following coefficients of correlation (r) were computed between annual fluctuations in growth and the combined temperatures for several groupings of months:

May to October (inclusive)	−0.124
June to September (inclusive)	.036
May and June	.218
May, June, and July	.268
May, June, and September	.416
May, June, and October	.104
May, June, September, and October	.352
May and July	.371
May, July, and September	.562
May and September	.550
May and October	.116
May, September, and October	.327
June, July, and August	−.289
June and August	−.461
June, August, and October	−.537
June and September	.328
June and October	−.176
June, September, and October	.202
July and August	−.384
July, August, and September	−.289
July and September	.651
August and October	−.420
September and October	.180

A detailed discussion is unnecessary, but attention is called to the following points:

1. There is no evidence of correlation between annual fluctuations in growth rate and in temperature during the season as a whole. The coefficients for the 6- and 4-month periods May-October and June-September were both low (−0.124 and 0.036).

2. Combinations of data for the 3 months, May, July, and September, which exhibited positive though statistically insignificant correlations of temperature and growth yielded evidence that a real correlation may exist. The coefficient for the three months combined was 0.562, and both of the groupings of two that included September—May and September ($r=0.550$), and July and September ($r=0.651$)—also showed significant positive correlation between temperature and growth. Only the coefficient for May and July ($r=0.371$) was below the significant value. It is to be noted also that the combinations of still other months with any of these three, or groupings of them, diminished the correlation below the significant level.

3. The negative coefficient of correlation between annual fluctuations in growth and the combined temperatures during the three months, June, August, and October, that exhibited negative values individually was significant ($r=-0.537$) but was less than the figure for August alone ($r=-0.605$). Furthermore, not one of the coefficients for the three pairings of these months—June and August ($r=0.461$), June and October ($r=-0.176$), and August and October ($r=-0.420$)—was significant. This behavior of the data suggests that any true negative correlation between growth and temperature during the growing seasons probably holds for August alone.

Inasmuch as earlier investigations have demonstrated that correlations among meteorological factors themselves can obscure true relations between those factors and growth (Hile 1941) or even render the data highly ambiguous (Van Oosten and Hile 1949), the possibility of similar interference was checked in the present data. This

work was carried out with special reference to the relation between the annual fluctuations of temperatures in June and in August and those of other months.

The lack of correlation between June temperatures and growth appears to be somewhat anomalous in view of the evidence of a positive correlation between growth and temperatures in May and July. Since the absolute temperature in June normally is intermediate between those of May and July a similar relation would be expected for all 3 months. The coefficients of correlation between temperatures in June and those in certain other months listed below are too small, however, to support any belief that a true relation between growth and June temperatures has been concealed by correlations with temperatures of other periods of the growing season.

Between June temperature and temperature in—

	Correlation
May and July	0. 291
May and September	. 214
May, July, and September	. 246
July and September	. 124
August	. 083

The high negative value of r for growth and August temperatures cannot be termed anomalous since water temperatures reach their maximum in that month in most years[11] and the concept that a high maximum might exert a depressing effect on growth is not unreasonable. It was considered desirable, nevertheless, to determine the possible effects on the interpretation of the data of correlations between August temperatures and those of months that exhibited significant positive correlations between temperature and growth. The following coefficients, including one for May and July in which temperature was not correlated significantly with growth, were computed.

Between August temperature and temperature in—

	Correlation
May and July	−0. 086
May and September	−. 186
July and September	−. 339
May, July, and September	−. 205

Again none of the correlations between temperatures in different periods was sufficiently close to conceal possible relations.

The data presented in this section may be taken as strong evidence that temperatures exert a significant effect on the annual fluctuations in growth of the yellow perch in Lake Erie, with high temperatures in May, July, and September (especially September) accelerating growth, and high temperatures in August retarding it.

Any attempt at a biological interpretation of the observed correlations would, with our present knowledge, be of little value. Conceivably, temperatures may affect growth directly, as through the control of the instantaneous rate of increase or of the length of the growing season, or indirectly, as through the control of the distribution or abundance of food organisms. Until more is learned of the natural history of the perch, the mechanism of the apparently significant correlation between growth and temperature must remain unknown.

[11] This statement is supported by records of Lake Erie water temperatures at the intake of the Chestnut Street Water Plant at Erie, Pa. (published in the Annual Reports of the Commissioner of Water Works of that city). According to those records the maximum monthly average water temperature occurred in August in 23 of the 25 years, 1923–47; furthermore, August temperatures of the period averaged 2.3° and 3.7° F. higher than those of July and September. The crib of the intake is located 5,100 feet north of the Presque Isle Peninsula and is covered by 22 feet of water at low-water level. Although Erie is located well to the east of the centers of greatest abundance of the yellow perch, water temperatures off that port may be taken to indicate monthly trends.

LENGTH-FREQUENCY DISTRIBUTION

The catches of impounding nets and gill nets differed in the actual form of the frequency distribution as well as in the size of fish taken (table 17). The length distribution of yellow perch caught in trap nets and pound nets was unimodal each year. The shoal-net collections, on the other hand, showed definite bimodal length distributions for 1927 and 1929, but gave no indication of bimodality in 1928. The fairly large number of small perch taken by the shoal nets during 1927 is probably explained by the presence of the abundant year class of 1926, then in their second year of life (age group I). The bimodal length distribution of the bull-net samples in 1927 was the result of the accidental capture of a large school of small fish on a single day. These smaller individuals ordinarily were not gilled in the true sense, but rather, were captured by tangling the webbing of the net in the marginal bones of the mouth or in the fins.

It will be noticed that there was considerable annual variation in the length of the modal fre-

TABLE 17.—*Length frequencies of Lake Erie yellow perch by year of capture and type of gear*

[An asterisk designates the modal interval in each frequency distribution]

Standard-length interval	Total length equivalent to midpoint	Taken by impounding nets								Taken by shoal gill nets [1]				Taken by bull gill nets [2]			
		1927	1928	1929	1930	1931	1932	1937	Total	1927	1928	1929	Total	1927	1928	1929	Total
	Inches																
41 to 50 mm	2.2										1		1				
51 to 60 mm	2.7										2		2				
81 to 90 mm	4.0											2	2				
91 to 100 mm	4.5			1					1	1		5	6		1		1
101 to 110 mm	5.0	4	1	31					36	9	1	13	23	4			4
111 to 120 mm	5.4	21	5	73	7				106	37	1	8	46	27	1		28
121 to 130 mm	5.9	46	19	61	40	14			180	64		5	69	*49			49
131 to 140 mm	6.3	108	94	108	158	108	1		677	49	4	4	57	35	1		36
141 to 150 mm	6.7	272	477	291	529	568	3	3	2,143	47	15	1	63	17	9	1	27
151 to 160 mm	7.2	380	1,143	563	1,016	1,167	1	10	4,270	26	11	1	38	4	14		18
161 to 170 mm	7.6	495	*1,531	1,021	*1,541	2,608	10	24	7,130	14	30	4	48	1	30	3	34
171 to 180 mm	8.1	*509	1,090	1,692	1,364	4,524	28	*35	9,242	13	84	27	124	3	40	5	48
181 to 190 mm	8.6	414	612	2,553	1,126	*4,963	*46	24	*9,738	31	241	165	437	6	79	15	100
191 to 200 mm	9.0	375	411	*2,632	759	3,608	27	19	7,831	130	708	987	1,825	13	136	78	227
201 to 210 mm	9.4	317	253	1,765	376	1,399	10	6	4,126	397	*866	*1,750	*3,013	40	*173	252	465
211 to 220 mm	9.9	164	98	775	121	381	6	6	1,551	*545	629	1,214	2,288	36	130	*300	*466
221 to 230 mm	10.3	82	29	263	44	103		4	525	237	200	443	880	16	46	150	212
231 to 240 mm	10.7	16	14	83	22	29	1		165	51	47	88	186	3	16	30	49
241 to 250 mm	11.2	17	2	28	10	8			65	16	12	24	52	1	4	4	9
251 to 260 mm	11.6	3	3	3	4	4			17	2	2	3	7	1	1		2
261 to 270 mm	12.1		2	2	1	3			8								
271 to 280 mm	12.5					1			1								
281 to 290 mm	13.0			4		3			7	1			1	1			1
291 to 300 mm	13.4		1						1								
301 to 310 mm	13.9	1							1								
Total		3,224	5,785	11,939	7,118	19,391	133	131	47,721	1,670	2,754	4,744	9,168	257	681	838	1,776
Average standard length (mm.)		177	170	187	174	182	186	181	180	201	203	207	205	167	200	212	201
Average total length (inches)		8.17	7.85	8.64	8.04	8.41	8.59	8.36	8.32	9.22	9.32	9.50	9.41	7.72	9.18	9.73	9.22
Percentage illegal (less than 8½ inches)		61.1	78.8	38.1	69.8	53.4	43.6	61.1	55.6	15.9	7.4	2.0	6.2	54.9	17.0	1.4	15.1

[1] Gill nets 22 meshes deep.

[2] Gill nets 100 meshes deep.

quency group in each gear. The modal frequency intervals of perch caught in impounding nets varied from 161–170 mm. (7.6 inches total length) in 1928 and 1930 to 191–200 mm. (9.0 inches total length) in 1929, or over a range of 30 mm. (1.4 inches). Annual fluctuations in the percentage occurrence of individuals in the several length intervals of the trap-net and pound-net catches of 1927–29, inclusive, are shown graphically in figure 8, which includes only the length range over which the representation was continuous. The years 1927 to 1929 were selected for graphic presentation because the year class of 1926 dominated the collections for each of those three years. The mode of the 1927 specimens caught in impounding nets was at a length 10 mm. greater than the mode of the 1928 collections. Since collections of both years were dominated by fish of the 1926 year class, one would expect the length of the modal frequency in 1928 to be greater than that in 1927. However, this discrepancy can be explained readily. It may be seen in table 21 that two age groups were well represented in the 1927 collections; age group I made up 48.9 percent and age group II made up 39.9 percent of the total. The 1928 collections were made up almost entirely (90.6 percent) of group-II fish. Approximately 95 percent of the 1927 specimens were taken in October and November whereas some 72 percent of the 1928 individuals were taken by the end of June. Thus, the 1926 year class (group I of 1927), had only a small part of a growing season in which to increase their lengths before the 1928 collections (in which the year class appeared as age group II) were made. Furthermore, the occurrence of large numbers of group-II fish in 1927 caused the length at maximum abundance in the combined collections of that year to be greater than that of the dominant age group (see table 19). Thus, the reduced abundance of fish older than the 1926 year class in 1928 and the short period of time intervening between the dates of collection of the 1927 and 1928 samples no doubt account for the shorter modal length in 1928.

The large modal length in 1929 may be attributed in great measure to the dominant 1926 year class which had completed approximately 2 full years' growth subsequent to the collection of the 1927 material. Even so, the length of the modal frequency in 1929 was somewhat less than the modal length of the 1926 year class (age group III) in that year because of the strong representation of the 1927 year class (age group II). In general, the position of the modal frequency each year can

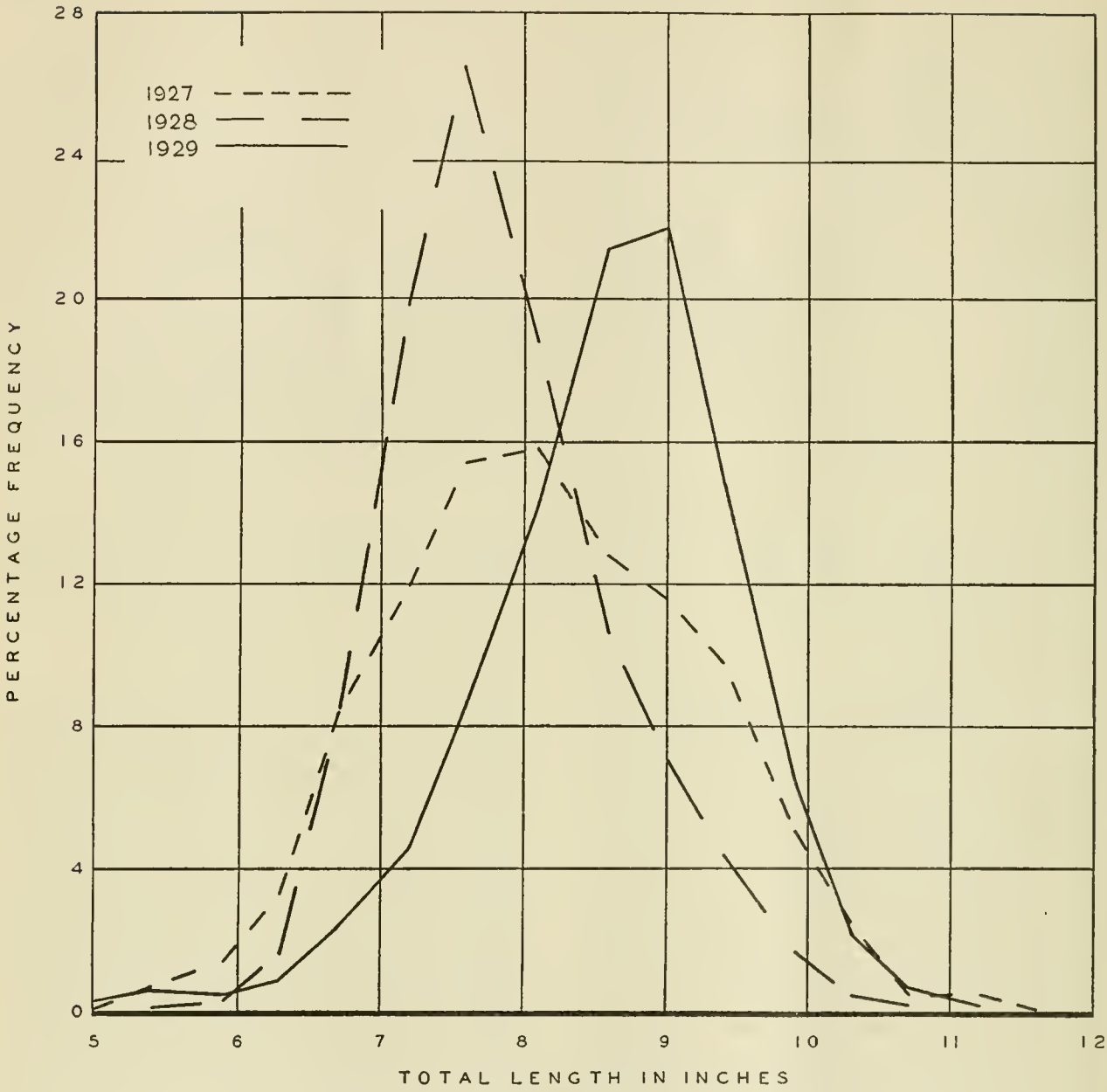

FIGURE 8.—Percentage frequency distribution of total length of Lake Erie yellow perch in 1927, 1928, and 1929 collections from impounding nets. Curves extend only over length range where representation was continuous.

be explained by the known age composition of the stock and the time of year when the collections were obtained. A similar explanation may account for the shifts in the modal frequency of the years 1930 to 1932 and 1937.

The gill-net collections showed trends in the annual fluctuation of the length at maximum abundance similar to those of the impounding nets, but the total range of variation of the length of the modal frequencies of the fish actually gilled was reduced. The modal frequency interval of the shoal-net samples varied only from 201–210 mm. (9.4 inches total length) in 1928 and 1929 to 211–220 mm. (9.9 inches total length) in 1927, or extended over a range of 10 mm. as compared with a range of 30 mm. in impounding-net samples. The modes of the yellow perch actually gilled by the bull net were at the 201–210 mm. (9.4 inches total length) interval in 1927 and 1928, and at the 211–220 mm. (9.9 inches total length) level in

1929. The reduction in the annual fluctuation of the position of the modal length intervals of the gilled fish in the gill-net collections as compared with the impounding-net samples can be ascribed to the greater selectivity of gill nets.

The lengths of the modal frequencies of fish gilled in both shoal and bull nets were without exception greater than those of fish caught in impounding nets in the same year. The general differences between the length distribution of the fish from impounding, shoal, and bull nets (all collections combined) are shown graphically in figure 9. The curves are based on the totals of table 17, expressed as percentage frequencies. The graph includes only the length range over which representation was continuous. As mentioned in the preceding paragraph, the much more compact distributions and the greater average size of perch in the gill-net collections may be attributed to net selectivity. The occurrence of small

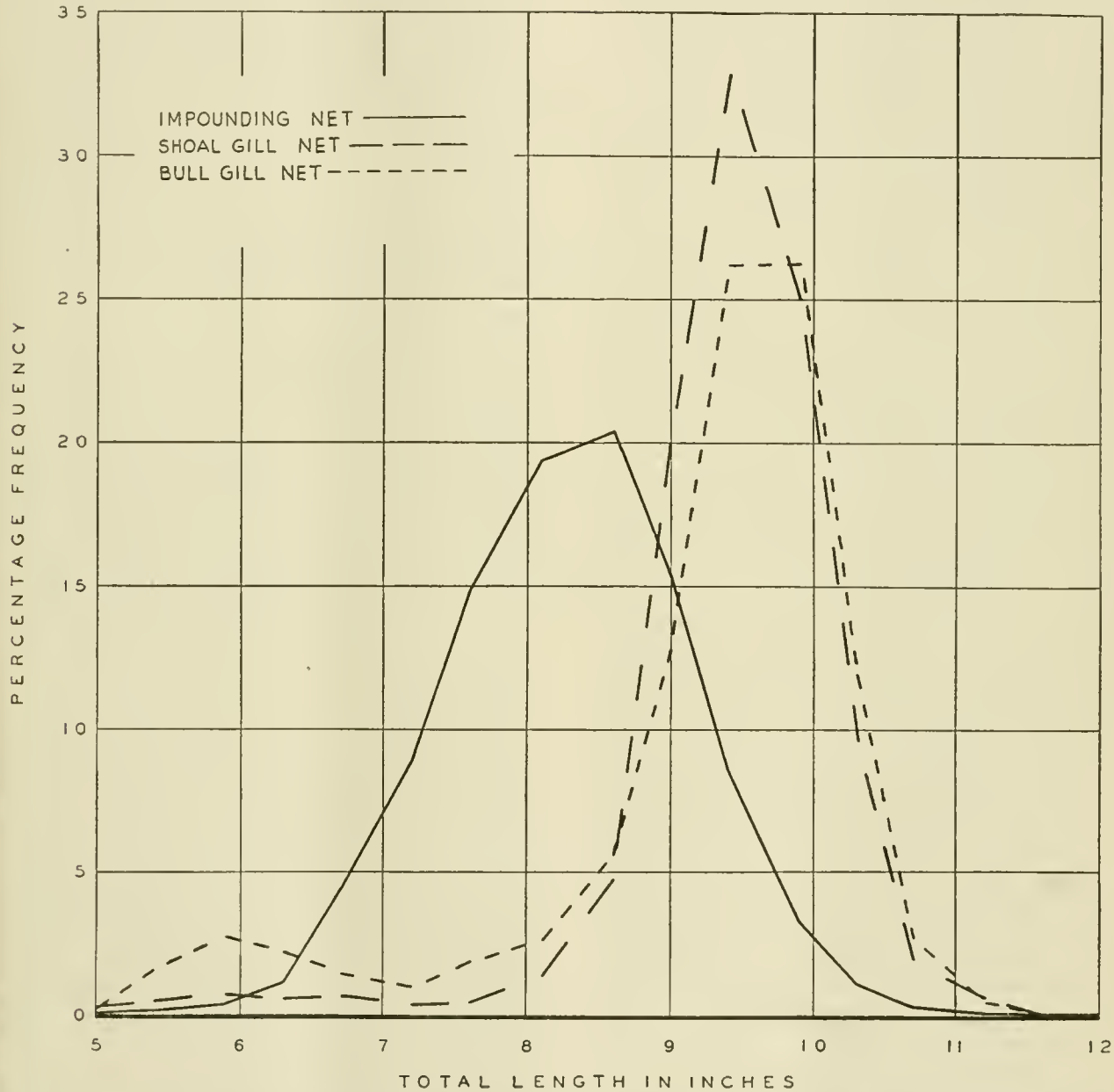

FIGURE 9.—Percentage frequency distribution of total lengths of Lake Erie yellow perch in collections from each kind of gear. Curves extend only over length range where representation was continuous.

perch in the gill-net collections does not represent gilling but, as stated earlier, is the result of the entanglement of the marginal bones of the mouth or of the fins in the gill-net webbing.

The occurrence of illegal-sized yellow perch in impounding-net samples (table 17) varied from a maximum of 78.8 percent in 1928 when the collections were dominated by the 1926 year class as age group II to a minimum of 38.1 percent in 1929 when the same year class was dominant as age group III. Had the computation for 1928 been made on the basis of the then-effective size limit of 9 inches instead of the current 8½ inches, the proportion of undersized yellow perch would have been even greater—89.6 percent. The 1927 collection which was dominated by the 1926 year class as age group I nevertheless had relatively fewer illegal-sized yellow perch (61.1 percent computed from a size limit of 8½ inches and 76.2 percent from a size limit of 9 inches) than the 1928 collection. An explanation of this discrepancy was given on page 237. Perch under the legal size limit were in the minority in the impounding-net samples in only 2 of 7 years (1929 and 1932). The percentage of undersized perch in the collections of all years combined, computed from a size limit of 8½ inches, was 55.6.

Illegal-sized yellow perch were relatively much less abundant in the gill-net than in the impounding-net catches, except in the 1927 bull-net samples which contained a high proportion of small, accidentally captured fish. Undersized individuals in shoal-net samples varied from a maximum of 15.9 percent in 1927 to a minimum of 2 percent in 1929 and amounted to 6.2 percent for the 3 years' collections combined. Computed from the then-effective size limit of 9 inches, the 1927 and 1928 percentages would have been higher—20.3 and 23.4. The percentages of undersized yellow perch in bull nets were 54.9 in 1927, 17.0 in 1928, and 1.4 in 1929. On the basis of the then-effective size limit of 9 inches these would have been increased to 59.1 and 33.2 percent in 1927 and 1928. For all years combined the percentage of illegal-sized yellow perch in the bull nets was 15.1 as compared with 6.2 in the shoal-net collections. The percentage of illegal-sized fish in all gill nets was 7.6.

The proportion of illegal-sized yellow perch in gill-net catches provides a fairly precise measure of the destruction of undersized individuals by this type of gear, as practically all individuals are dead at capture or are killed in the process of removal from the nets. It should be noted, however, that on the average the percentage of undersized fish in gill-net samples usually fell well below Ohio's legal allowance of 10 percent in the commercial catch, especially since the allowance is based on weight rather than on numbers of fish.

The destruction of illegal-sized yellow perch can be determined less accurately for impounding nets than for gill nets because the trap-net and pound-net fishermen are required to return all illegal-sized fish to the water. It is relatively certain that an unknown portion of these fish die as the result of handling. It is known that on the average 14 percent of the illegal-sized perch taken by Lake Erie trap nets are dead at the time of lifting. (See footnote 5, p. 221.) Since 55.6 percent of the yellow perch from impounding nets were undersized, it may be computed that for every 1,000 yellow perch taken, 76 illegal-sized fish were destroyed. This value was well below the 151 determined for bull nets but was above the 62 for shoal nets, and equaled the 76 from all gill nets. However, the computed number of illegal-sized yellow perch destroyed by impounding nets must be considered as the minimum since it does not include those fish that are killed during the sorting of the catch to conform to the legal-size limit. Further, impounding nets took many more fish during the year than did the gill nets and therefore destroyed many more individuals. The data seem to offer good support to Van Oosten's (1936) conclusion that more fish are destroyed by trap nets than by gill nets.

The importance of the destruction of small yellow perch by trap nets is emphasized when it is remembered that in recent years this gear has accounted for approximately 61 percent of all perch taken in the United States waters of Lake Erie (65 percent of those taken in Ohio waters).[12]

Table 18 contains a summary of the length frequencies (total lengths) by half-inch intervals, the percentage frequencies, and the cumulative percentages for Lake Erie yellow perch taken in different types of gear, with all years' collections combined. Practical considerations make such

[12] Percentages were computed from data for the calendar years 1930, 1931, 1932, 1934, 1936, 1937, and 1938 contained in the former U. S. Bureau of Fisheries publication, "Fisheries Industries of the United States," Report of the Commissioner of Fisheries, for 1931, 1932, 1933, 1935, 1937, 1938, and 1939.

TABLE 18.—*Length frequencies of Lake Erie yellow perch taken in different types of gear*

[Collections of all years combined]

Total-length interval [1]	Trap and pound nets			Shoal gill nets			Bull gill nets		
	Number of specimens	Percentage	Cumulative percentage	Number of specimens	Percentage	Cumulative percentage	Number of specimens	Percentage	Cumulative percentage
2.0 to 2.5 inches				1	0.01	0.01			
2.5 to 3.0 inches				2	.02	.03			
3.0 to 3.5 inches						.03			
3.5 to 4.0 inches						.03			
4.0 to 4.5 inches	1	[2]	[2]	4	.04	.07			
4.5 to 5.0 inches	7	0.01	0.01	14	.15	.22	2	0.11	0.11
5.0 to 5.5 inches	98	.21	.22	46	.50	.72	18	1.01	1.12
5.5 to 6.0 inches	130	.27	.49	54	.59	1.31	40	2.25	3.37
6.0 to 6.5 inches	664	1.39	1.88	85	.93	2.24	51	2.87	6.24
6.5 to 7.0 inches	1,872	3.92	5.80	57	.62	2.86	33	1.86	8.10
7.0 to 7.5 inches	5,182	10.86	16.66	48	.52	3.38	22	1.24	9.34
7.5 to 8.0 inches	8,109	16.99	33.65	62	.68	4.06	40	2.25	11.59
8.0 to 8.5 inches	10,473	21.95	55.60	194	2.12	6.18	63	3.55	15.14
8.5 to 9.0 inches	11,346	23.78	79.38	1,004	10.95	17.13	156	8.78	23.92
9.0 to 9.5 inches	6,189	12.97	92.35	2,947	32.14	49.27	390	22.47	46.39
9.5 to 10.0 inches	2,634	5.52	97.87	3,156	34.42	83.69	594	33.45	79.84
10.0 to 10.5 inches	751	1.57	99.44	1,248	13.61	97.30	297	16.72	96.56
10.5 to 11.0 inches	174	.36	99.80	193	2.11	99.41	50	2.82	99.38
11.0 to 11.5 inches	65	.14	99.94	50	.56	99.97	8	.45	99.83
11.5 to 12.0 inches	11	.02	99.96	2	.02	99.99	2	.11	99.94
12.0 to 12.5 inches	6	.01	99.97			99.99			
12.5 to 13.0 inches	3	.01	99.98			99.99			
13.0 to 13.5 inches	4	.01	99.99	1	.01	100.00	1	.06	100.00
13.5 to 14.0 inches	2	[2]	100.00						

[1] Each ½-inch interval contains lengths up to but not including the greater value.
[2] Specimens occurred in the samples but made up less than 0.005 percent of the total.

a tabulation desirable since legal-size limits for yellow perch are expressed in terms of the total length in inches. It may be seen at a glance, for example, that with a size limit of 8½ inches, 55.6 percent of the yellow perch taken in trap nets were under legal length, whereas 79.38 percent were undersized with a 9-inch limit; or it may be seen that almost 98 percent of the yellow perch in trap-net catches were less than 10 inches long. The tabulation also permits ready comparisons of the catches by different types of gear.

The length distributions by age for impounding-net samples are shown in table 19. The collections of 1930, 1932, and 1937 are omitted from the table because the number of specimens whose ages were determined was too small in each of those years to give reliable results. The length range of fish of the same age did not vary greatly in the better-represented age groups during the 3 years 1927 to 1929. The range in length of the age groups was sufficiently great to cause considerable overlapping between these groups. Because of this overlap, length cannot be held a reliable indication of age. Age groups IV and V were represented by too few individuals to give an accurate idea of the range in either group. The distinctly unimodal distribution within each well-represented age group and the great amount of overlapping in length probably accounted for the unimodal length distribution in the yearly collections from impounding nets.

Additional data obtained from impounding nets each year in the period 1944–48 (table 20) make possible a comparison of the length distribution of the legal-sized yellow perch in the commercial catch of those years with the legal-sized fish included in the biological samples collected from the same type of nets in the 3 years 1927 to 1929. Only age groups II and III will be compared since younger and older fish contributed but little to the commercial catch.

The length distribution of the legal-sized (8½ inches total length and larger) yellow perch assigned to age group II exhibited a striking difference between the two periods, 1927–29 and 1944–48. The minimum legal size of 8½ inches was near, or above, the modal length of all group-II fish in each of the 3 years 1927 to 1929. The length distribution of group-II fish in each year of the period 1944–48 gave strong reason to believe that the 8½-inch size limit was below (less than) the modal length each year with the possible exception of 1945 when the small sample agreed more nearly with the data of the earlier period. Also in each year except 1945 of the recent period, age group II contained longer fish than in any year of the earlier period. Further, the number of the longer group-II fish tended to

TABLE 19.—*Length frequencies of Lake Erie yellow perch by age and year of capture, taken by impounding nets from western and middle Lake Erie*

[An asterisk designates the modal interval in each frequency distribution]

Standard-length interval	Total length equivalent to midpoint	Age group I			Age group II			Age group III			Age group IV			Age group V		All age groups
		1927	1928	1929	1927	1928	1929	1927	1928	1929	1927	1928	1929	1927	1929	
	inches															
106 to 110 mm.	5.1		1	1												2
111 to 115 mm.	5.3		2													2
116 to 120 mm.	5.5			1		1										2
121 to 125 mm.	5.8			1												1
126 to 130 mm.	6.0	1	2	3	2											8
131 to 135 mm.	6.1	3	1	3												7
136 to 140 mm.	6.4	7		6			1									14
141 to 145 mm.	6.6	16		13	3	3	3									38
146 to 150 mm.	6.8	18	2	*16	5	11	2			1						55
151 to 155 mm.	7.1	23		5	4	29	7									68
156 to 160 mm.	7.3	25		11	8	41	20	1								106
161 to 165 mm.	7.5	32		7	14	58	21	1	1							134
166 to 170 mm.	7.8	*52	1	9	14	80	34	2	3	4						199
171 to 175 mm.	8.0	37	2	6	*27	99	35	3	4	10						*223
176 to 180 mm.	8.2	13		1	21	*122	27	3	6	18						211
181 to 185 mm.	8.5	5			*27	108	*42	3	6	31	1					*223
186 to 190 mm.	8.7	2			20	100	39	5	4	31		1	2			204
191 to 195 mm.	8.9	1			18	77	33	*8	3	52			5			197
196 to 200 mm.	9.1				10	49	39	2	10	70		1	8			189
201 to 205 mm.	9.3				11	28	27	5	*11	72	2		7			163
206 to 210 mm.	9.5				3	15	21	5	8	*75			5		1	133
211 to 215 mm.	9.8				3	7	16	5	4	68			3			106
216 to 220 mm.	10.0				2	3	4		4	68			7			88
221 to 225 mm.	10.1					1	1	3	2	51		1	*12			71
226 to 230 mm.	10.4							1	1	36			2		1	41
231 to 235 mm.	10.6								2	15	1	1	5		1	25
236 to 240 mm.	10.8									16		1	4			21
241 to 245 mm.	11.1									10	1		1			12
246 to 250 mm.	11.3									2				2		4
251 to 255 mm.	11.5									2						2
256 to 260 mm.	11.7								1							1
Total		235	11	83	192	832	372	47	70	632	5	5	61	2	3	2,550
Average standard length (mm.)		162	138	152	181	179	182	195	198	207	214	217	214	250	223	186
Average total length (inches)		7.5	6.4	7.0	8.4	8.3	8.4	9.0	9.1	9.5	9.8	10.0	9.8	11.4	10.1	8.6
Percent illegal (less than 184 mm.)		97.9	100.0	100.0	59.4	61.2	47.0	25.5	25.7	8.2	20.0	0	0	0	0	47.2

TABLE 20.—*Length frequencies of legal-sized yellow perch taken commercially and as biological samples in impounding nets in western and middle Lake Erie*

Total-length interval [1]	Standard-length interval	1927 [2]	1928 [2]	1929 [2]	1944 [2]	1945 [2]	1946 [3]	1947 [3]	1948 [3]	Years combined	
										1927–29	1944–48
Age group II:	*Millimeters*										
8.50 to 8.75 inches	184 to 189	28	119	44	6	13	8	13	19	191	59
8.75 to 9.00 inches	190 to 195	20	104	43	10	13	8	22	37	167	90
9.00 to 9.25 inches	196 to 201	11	54	45	17	6	34	50	65	110	172
9.25 to 9.50 inches	202 to 206	11	28	26	15	6	53	24	48	65	146
9.50 to 9.75 inches	207 to 211	2	12	18	12	8	26	32	62	32	140
9.75 to 10.00 inches	212 to 217	4	7	16	6	1	17	9	28	27	61
10.00 to 10.25 inches	218 to 224	1	3	3	2		7	9	29	7	47
10.25 to 10.50 inches	225 to 230						1	2	3		6
10.50 to 10.75 inches	231 to 236				1			2	7		10
10.75 to 11.00 inches	237 to 241								1		1
Total number		77	327	195	69	47	154	163	299	599	732
Average total length (inches)		8.95	8.86	9.07	9.37	9.10	9.45	9.28	9.39	8.94	9.36
Age group III:											
8.50 to 8.75 inches	184 to 189	3	5	41		1		2	1	49	4
8.75 to 9.00 inches	190 to 195	11	4	58		6		11	1	73	18
9.00 to 9.25 inches	196 to 201	4	12	84	4	17	2	30	20	100	73
9.25 to 9.50 inches	202 to 206	4	12	69	5	18	5	21	20	85	69
9.50 to 9.75 inches	207 to 211	5	5	75	1	17	16	32	28	85	94
9.75 to 10.00 inches	212 to 217	4	6	93	2	14	12	14	16	103	58
10.00 to 10.25 inches	218 to 224	2	3	68		7	9	15	9	73	40
10.25 to 10.50 inches	225 to 230	2	2	51		2	3	4		55	9
10.50 to 10.75 inches	231 to 236		2	21		3	1	4	2	23	10
10.75 to 11.00 inches	237 to 241			12			2		1	12	3
11.00 to 11.25 inches	242 to 247			8				1		8	1
11.25 to 11.50 inches	248 to 252			3						3	
11.50 to 11.75 inches	253 to 258		1	1					3	2	3
Total number		35	52	584	12	85	50	134	101	671	382
Average total length (inches)		9.29	9.45	9.63	9.46	9.63	9.95	9.51	9.63	9.60	9.62

[1] Each interval contains lengths up to but not including the greatest value. [2] From biological samples. [3] From commercial samples.

increase in the later years of the 1944–48 period. The average total length of the legal-sized group-II yellow perch was considerably larger in each year except 1945, of the period 1944–48, than in any year of the period 1927–29.

The totals for the two periods place the modal length of the legal-sized fish in the 8.50 to 8.75 inch interval in 1927–29 and in the 9.00 to 9.25 inch interval in 1944–48. The weighted-average total lengths for the two periods were 8.94 and 9.36 inches, respectively. The use of unweighted means of the annual average total lengths to eliminate the distorting effects of the differences in size of samples changes the averages for the periods only slightly, to 8.96 and 9.32 inches. Both methods of computation show that the age-group-II fish of legal size taken in 1944–48 averaged about 0.4 inch longer than those taken in 1927–29.

The general pattern of the length distribution of the legal-sized yellow perch assigned to age group III failed to show as great differences between the 1927–29 and 1944–48 periods as were exhibited by group-II fish. The modal frequency interval was well above the 8½-inch size limit in all years. The average total length was greater each year in the 1944–48 period than in either 1927 or 1928 but agreed rather well with that of 1929. The weighted-average length was almost identical in both periods because the best represented year in the earlier period included fish with the longest average length while the best represented of the later years included specimens with the shortest average for the period. The unweighted means of the annual averages in the two periods were 9.46 and 9.64 inches. The more reliable unweighted means thus show the legal-size yellow perch assigned to age group III to have averaged approximately 0.2 inch longer in 1944–48 than in 1927–29.

Although these data do not constitute proof, they do offer strong evidence that yellow perch in Lake Erie were growing at a faster rate in 1944–48 than in 1927–29.

AGE COMPOSITION AND ABUNDANCE OF YEAR CLASSES

In the study of the age and year-class composition of the Lake Erie yellow perch it should be remembered that the samples must be considered truly descriptive, not of the stock, but rather of the catch of commercial gear. Trap-net and pound-net collections were employed in the biological study of the relative abundance of age groups and year classes because those nets are less selective than gill nets. Although samples from impounding nets in a single year may not give dependable information as to the relative abundance of the year classes represented, the persistent abundance or scarcity of a year class at different ages, that is, in different years' collections, offers a reasonably trustworthy method for the detection of exceptionally strong or weak year classes. Of course, a knowledge of the age composition in both gill nets and impounding nets is of importance in the practical problem of determining the effects of these types of gear on the stock.

The number of specimens and the percentage occurrence of each age group in the yearly collections of biological samples from impounding nets for the years 1927–37 are shown in table 21. Age group I dominated the samples in one (1927) of the six years in which collections were made, although the percentage of abundance of this age group was also high in 1937. Age group II dominated in three years (1928, 1930, and 1937), and group III was dominant in the remaining two years (1929 and 1932). However, the fact that the 1932 samples were taken from the spawning run in April, when the fish were comparable in size and maturity to those in the next younger age group in the previous fall, throws doubt on the validity of comparisons between the data for this and other years. The spawning run consists almost entirely of mature individuals; consequently, those age groups containing high percentages of immature fish were not represented adequately in the 1932 collections. The 1932 data serve, however, to show the age composition of the catch in the spawning-run fishery.

It will be brought out later (p. 251) that unusual conditions made possible the dominance of age group I in 1927 and of age group III in 1929. Dominance of age group II in the late-season catch of yellow perch in impounding nets may be considered the normal condition.

The preceding remarks were based on the total catch of impounding nets including both legal-

TABLE 21.—*Distribution by age groups of yellow perch in the different years' collections from impounding nets*

[Percentages in parentheses]

Year	Month of capture	Number of specimens	Number and percentage in age group—				
			I	II	III	IV	V
1927	October and November	481	235 (48.9)	192 (39.9)	47 (9.8)	5 (1.0)	2 (0.4)
1928	July, August, September, October, and November	918	11 (1.2)	832 (90.6)	70 (7.6)	5 (0.5)	
1929	July, August, September, November, and December [1]	1,151	83 (7.2)	372 (32.3)	632 (54.9)	61 (5.3)	3 (0.3)
1930	July and September	222	1 (0.4)	172 (77.5)	45 (20.3)	4 (1.8)	
1932	April	133		2 (1.5)	98 (73.7)	33 (24.8)	
1937	November	131	62 (47.3)	66 (50.4)	3 (2.3)		
	All collections	3,036	392 (12.9)	1,636 (53.9)	895 (29.5)	108 (3.6)	5 (0.2)

[1] The 1929 data may be considered as representative of autumn conditions since 66 percent of the specimens were collected in November and December.

sized and illegal-sized fish. It is of practical value to know also the representation of these two size groups separately as well as the age groups in the marketable catch, that is, legal-sized fish. Data on these subjects are contained in table 22 which shows the number and percentage of legal and undersized yellow perch in each age group represented in the total catch and in table 23 which gives the numerical and percentage composition of the marketable catch in each year's collection. From the former table it may be seen that legal-sized yellow perch constituted an unimportant proportion of age group I. This age group dominated the catch of impounding nets in 1927 but apparently contributed nothing to the commercial yield. The highest percentage of legal-sized perch in any group I was 8.1 in 1937. The majority of all group-II perch captured were undersized—60.3 percent as determined from a size limit of 8½ inches. In only two years (1929 and 1937) did the percentage of undersized perch in age group II fall below 50. Thus it may be seen that the age group that normally dominated the catch of impounding nets (the spawning-run fishery excepted) consisted largely of yellow perch that could not be retained and sold by the fisherman. The percentage of undersized perch in all group-III fish combined was small (15.1). In two years

TABLE 22.—*Distribution by age groups of legal- and illegal-sized yellow perch in the different years' collections from impounding nets*

[Percentages in parentheses]

Year	Minimum legal-size limit (inches)	Number of specimens	Number of legal in all ages	Number of illegal in all ages	Number and percentage in age group—									
					I		II		III		IV		V	
					Legal	Illegal	Legal	Illegal	Legal	Illegal	Legal	Illegal	Legal	Illegal
1927	9	481	56 (11.6)	425 (88.4)	0 (0)	235 (100.0)	29 (15.1)	163 (84.9)	21 (44.7)	26 (55.3)	4 (80.0)	1 (20.0)	2 (100.0)	0 (0)
	8½	481	123 (25.6)	358 (74.4)	4 (1.7)	231 (98.3)	77 (40.1)	115 (59.1)	35 (74.5)	12 (25.5)	5 (100.0)	0 (0)	2 (100.0)	0 (0)
1928	9	918	151 (16.4)	767 (83.6)	0 (0)	11 (100.0)	103 (12.4)	729 (87.6)	44 (62.7)	26 (37.1)	4 (80.0)	1 (20.0)		
	8½	918	384 (41.8)	534 (48.2)	0 (0)	11 (100.0)	327 (39.3)	505 (60.7)	52 (74.3)	18 (25.7)	5 (100.0)	0 (0)		
1929	8½	1,151	843 (73.2)	308 (26.8)	0 (0)	83 (100.0)	195 (52.4)	177 (47.8)	584 (92.4)	48 (7.6)	61 (100.0)	0 (0)	3 (100.0)	0 (0)
1930	8½	222	54 (24.3)	168 (75.7)	0 (0)	1 (100.0)	9 (5.2)	163 (94.8)	41 (91.1)	4 (8.9)	4 (100.0)	0 (0)		
1932	8½	133	74 (55.6)	59 (44.4)			0 (0)	2 (100.0)	45 (45.9)	53 (54.1)	29 (87.9)	4 (12.1)		
1937	8½	131	50 (38.2)	81 (61.8)	5 (8.1)	57 (91.9)	42 (63.6)	24 (36.4)	3 (100.0)	0 (0)				
Total: Effective limits [1]	(1)	3,036	1,228 (40.4)	1,808 (59.6)	5 (1.3)	387 (98.7)	378 (23.1)	1,258 (76.9)	738 (82.5)	157 (17.5)	102 (94.4)	6 (5.6)	5 (100.0)	0 (0)
8½-inch limit [2]	8½	3,036	1,528 (50.3)	1,508 (49.7)	9 (2.3)	382 (97.7)	650 (39.7)	986 (60.3)	760 (84.9)	135 (15.1)	104 (96.3)	4 (3.7)	5 (100.0)	0 (0)

[1] The number and percentage of legal- and illegal-sized fish in the various age groups of all years' collections combined as determined for the size limit effective in each year.

[2] As determined for 8½-inch limit for all years.

(1927 and 1932), however, this percentage exceeded 50. The proportion of undersized perch in age group IV may be considered unimportant, and all group-V perch were of legal size.

The effects of the varying percentages of legal and undersized yellow perch in the different age groups, and of the varying abundance of the age groups themselves, on the age composition of the marketable catch may be seen in table 23. Age group II dominated the commercial catch in all years' samples except four, 1929, 1930, 1932, and 1945, when group-III fish were most numerous. The data in table 23 give strong indication that the time of capture within the season may have an important effect on the age composition of the marketable catch. The April 1932 (spawning-run) sample contained no legal-sized yellow perch younger than age group III. The midsummer collection of 1930 (most of the fish were taken in July) was dominated by age group II when both legal and undersized yellow perch were included (table 22). However, such a small proportion (5.2 percent) of the age group had attained legal size (table 22) that age group III became strongly dominant (75.9 percent) when only legal-sized fish were considered (table 23). Of the 10 years in which all or most of the yellow perch were taken in autumn (1927, 1928, 1929, 1937, 1943–48), after the continued growth of group-II perch had brought a greater proportion of them to legal length, this group dominated the commercial catch in all but 1929 and 1945. Since the conditions are known to have been abnormal in 1929, and perhaps also in 1945, it appears valid to conclude that age group II normally dominates the late-season commercial catch. Members of the same year class dominate the fishery as age group III the following spring and during the summer up to the point that the growth of the incoming group II makes it possible for fish of that age to assume a dominant position in the commercial catch.

TABLE 23.—*Distribution by age groups of legal-sized yellow perch in the different years' collections from impounding nets*

[Percentages in parentheses]

Year	Legal size limit [1] (inches)	Number of specimens	Number and percentage in age group—				
			I	II	III	IV	V
1927	9	56	0 (0)	29 (51.8)	21 (37.5)	4 (7.1)	2 (3.6)
	8½	123	4 (3.2)	77 (62.6)	35 (28.5)	5 (4.1)	2 (1.6)
1928	9	151	0 (0)	103 (68.2)	44 (29.1)	4 (2.7)	0 (0)
	8½	384	0 (0)	327 (85.2)	52 (13.5)	5 (1.3)	0 (0)
1929	8½	843	0 (0)	195 (23.1)	584 (69.3)	61 (7.2)	3 (0.4)
1930	8½	54	0 (0)	9 (16.7)	41 (75.9)	4 (7.4)	0 (0)
1932	8½	74	0 (0)	0 (0)	45 (60.8)	29 (39.2)	0 (0)
1937	8½	50	5 (10.0)	42 (84.0)	3 (6.0)	0 (0)	0 (0)
1943	8½	28	6 (21.4)	16 (57.1)	5 (17.9)	1 (3.6)	0 (0)
1944	8½	81	0 (0)	69 (85.2)	12 (14.8)	0 (0)	0 (0)
1945	8½	153	0 (0)	47 (30.7)	85 (55.6)	19 (12.4)	2 (1.3)
1946	8½	213	0 (0)	154 (72.3)	50 (23.5)	7 (3.3)	2 (0.9)
1947	8½	320	1 (0.3)	163 (50.9)	134 (41.9)	19 (6.0)	3 (0.9)
1948	8½	420	7 (1.7)	299 (71.2)	101 (24.0)	13 (3.1)	0 (0)
Total	(1)	2,443	19 (0.8)	1,126 (46.1)	1,125 (46.0)	161 (6.6)	12 (0.5)
Average (unweighted) percentage:							
Effective limits.[1]	(1)	.....	(2.8)	(50.9)	(38.0)	(7.7)	(0.6)
8½-inch limit.[2]	8½	.....	(3.0)	(53.3)	(36.0)	(7.3)	(0.4)

[1] Minimum legal size 9 inches in 1927 and 1928 and 8½ inches in all other years.
[2] As determined for 8½-inch limit for all years.

The conclusion about the change in the age composition of the marketable catch within a single season finds further support in data of the 1928 and 1929 collections. Scales were collected in both summer and autumn of each of these years. Comparisons of the percentage age composition of legal-sized perch in different months of capture in the two years may be found in table 24. Analyses were made for the 1928 data with respect to the then-effective 9-inch size limit and the current 8½-inch limit. The data of table 24 cannot be considered descriptive of the typical seasonal changes in the age composition of legal-sized yellow perch since age group II was abnormally abundant in 1928 and group III was exceptionally strong in 1929. The percentages serve, nevertheless, to show clearly the tendency for group II to replace group III in the marketable catch as the season progresses. In 1928, age group III was dominant among legal-sized yellow perch in July (41.7 percent) but age group II was dominant in the later months of the season. Had an 8½-inch limit been in force, age group II would have dominated the catch in July as well as in late season, but its relative importance would have increased, nevertheless, from 69.1 percent in July to 91.1 percent in August to November. The great abundance of group-III yellow perch in 1929 made it possible for that age group to maintain its dominance in the marketable catch

TABLE 24.—*Percentage age composition of legal-sized yellow perch in Lake Erie in different months of capture in 1928 and 1929*

Size limit and month of capture	Age group			
	II	III	IV	V
1928:				
9-inch size limit:				
July	33.3	41.7	25.0	0
August through November	71.6	27.7	.7	0
8½-inch size limit:				
July	69.1	21.4	9.5	0
August through November	91.1	8.6	.3	0
1929: 8½-inch size limit:				
July	.8	85.5	12.9	.8
August and September	14.4	85.6	0	0
November and December	31.6	59.4	8.6	.4

to the end of the season. The representation of age group II increased, however, from 0.8 percent in July to 14.4 percent in August and September and to 31.6 percent in November and December. At the same time the corresponding percentage representations of age group III changed from 85.5 to 85.6 to 59.4.

The legal-sized fish of the combined samples for all years' collections belonged very largely (92.1 percent) to age groups II and III which were represented almost equally—46.1 and 46 percent (table 23). However, the relatively high representation of age group III can be traced to the large 1929 collection in which it was dominant. A more reliable estimate of the age composition of the marketable catch may be had from the unweighted averages of the percentages for the different years. At the bottom of table 23 these averages are given as computed from the size limits actually in effect in the different years (that is, from a size limit of 9 inches in 1927 and 1928 and of 8½ inches in the later years) and as computed from a size limit of 8½ inches for all years. The percentages computed from both the effective and the 8½-inch size limits showed dominance of age group II.

Yellow perch older than age group V were not found in the samples, but are known to have been present in Lake Erie. Specimens selected because of their large size revealed no males older than age group IV, but did include one female of age group VII and two fish of undetermined sex assigned to age group VIII.

The data on the age composition of gill-net catches (shoal and bull nets) contained in tables 25, 26, and 27 correspond to those already given for trap nets. The data for 1927 and 1928 included both legal- and illegal-sized fish while those for later years represented only the commercial sizes. Comparisons between the catches of trap nets and gill nets bring out sharply the strongly selective action of the latter gear. Age group III dominated three of the four gill-net collections obtained in 1927 and 1928 (table 25). The fourth (the bull-net collection of 1928) was dominated by age group II, but age group III was only slightly less abundant. This distribution of the age groups bears little resemblance to the age composition of the less-selective impounding nets (table 21) where the 1927 samples were dominated by age group I (48.9 percent), and 90.6 percent of the yellow perch in the 1928 collections were members of age group II. The 1927 gill-net samples do not give the slightest indication of the great abundance of age group I. Possibly the dominance of age group II in the 1928 bull-net collection was due to the great abundance of group-II fish in that year. However, the shoal-net collection failed to reveal such dominance and abundance. On the whole, the age composition of gill-net catches appears to be in large measure independent of the relative strength of the age groups in the population. Characteristically, age group III was dominant, with age group II regularly well represented and occasionally dominant. The tendency for gill nets to take older fish than do trap nets may be seen also in the greater abundance of group-IV yellow perch in the gill-net samples.

A second difference between gill-net and impounding-net collections lies in the greater proportion of legal-sized yellow perch in the age groups from the former gear (table 26). For example, the percentages of legal yellow perch of group II, in the impounding-net collections for 1927 and 1928, were only 15.1 and 12.4, computed from a 9-inch size limit (table 22). Group II in the gill-net collections for these years, on the other hand, contained from 30.2 to 79.2 percent of such perch and showed an average for the 2-year period (bull and shoal nets combined) of 47.9 percent. If the percentages of legal-sized yellow perch in age group II are computed from a size limit of 8½ inches, the values are 39.7 for impounding-net samples and 76.3 for gill-net collections. A similar though less pronounced difference existed between the percentages of group III legal-sized

TABLE 25.—*Distribution by age groups of yellow perch from gill nets*

[Percentages in parentheses]

Year	Month of capture	Number of specimens	Number and percentage in age group—				
			I	II	III	IV	V
Taken in shoal nets:							
1927	August	84	2 (2.4)	29 (34.5)	40 (47.6)	11 (13.1)	2 (2.4)
1928	July and August	144	----------	53 (36.8)	73 (50.7)	17 (11.8)	1 (0.7)
Total		228	2 (0.9)	82 (36.0)	113 (49.6)	28 (12.3)	3 (2.9)
Taken in bull nets:							
1927	August	69	----------	24 (34.8)	38 (55.1)	5 (7.2)	2 (2.9)
1928	July and August	133	1 (0.8)	63 (47.4)	56 (42.1)	13 (9.8)	----------
Total		202	1 (0.5)	87 (43.1)	94 (46.5)	18 (8.9)	2 (1.0)
Take of shoal and bull nets combined:							
1927	August	153	2 (1.3)	53 (34.6)	68 (51.0)	16 (10.5)	4 (2.6)
1928	July and August	277	1 (0.4)	116 (41.9)	129 (46.6)	30 (10.8)	1 (0.4)
Total		430	3 (0.7)	169 (39.3)	207 (48.1)	46 (10.7)	5 (1.2)

TABLE 26.—*Distribution by age groups of legal- and illegal-sized yellow perch from gill nets*

[Percentages in parentheses]

Year and minimum legal size	Number of specimens	Number legal size	Number illegal size	Number and percentage in age group—									
				I		II		III		IV		V	
				Legal	Illegal	Legal	Illegal	Legal	Illegal	Legal	Illegal	Legal	Illegal
Taken in shoal nets:													
1927:													
9 inches	84	72	12	0 (0)	2 (100.0)	19 (65.5)	10 (34.5)	40 (100.0)	0 (0)	11 (100.0)	0 (0)	2 (100.0)	0 (0)
8½ inches	84	78	6	0 (0)	2 (100.0)	25 (86.2)	4 (13.8)	40 (100.0)	0 (0)	11 (100.0)	0 (0)	2 (100.0)	0 (0)
1928:													
9 inches	144	101	43	----------	----------	24 (45.3)	29 (54.7)	60 (82.2)	13 (17.8)	16 (94.1)	1 (5.9)	1 (100.0)	0 (0)
8½ inches	144	135	9	----------	----------	44 (83.0)	9 (17.0)	73 (100.0)	0 (0)	17 (100.0)	0 (0)	1 (100.0)	0 (0)
Total, 1927–28:													
9 inches	228	173	55	0 (0)	2 (100.0)	43 (52.4)	39 (47.6)	100 (88.5)	13 (11.5)	27 (96.4)	1 (3.6)	3 (100.0)	0 (0)
8½ inches	228	213	15	0 (0)	2 (100.0)	69 (84.1)	13 (15.9)	113 (100.0)	0 (0)	28 (100.0)	0 (0)	3 (100.0)	0 (0)
Taken in bull nets:													
1927:													
9 inches	69	64	5	----------	----------	19 (79.2)	5 (20.8)	38 (100.0)	0 (0)	5 (100.0)	0 (0)	2 (100.0)	0 (0)
8½ inches	69	68	1	----------	----------	23 (95.8)	1 (4.2)	38 (100.0)	0 (0)	5 (100.0)	0 (0)	2 (100.0)	0 (0)
1928:													
9 inches	133	75	58	0 (0)	1 (100.0)	19 (30.2)	44 (69.8)	43 (76.8)	13 (23.2)	13 (100.0)	0 (0)	----------	----------
8½ inches	133	101	32	0 (0)	1 (100.0)	37 (58.7)	26 (41.3)	51 (91.1)	5 (8.9)	13 (100.0)	0 (0)	----------	----------
Total, 1927–28:													
9 inches	202	139	63	0 (0)	1 (100.0)	38 (43.7)	49 (56.3)	81 (86.2)	13 (13.8)	18 (100.0)	0 (0)	2 (100.0)	0 (0)
8½ inches	202	169	33	0 (0)	1 (100.0)	60 (69.0)	27 (31.0)	89 (94.7)	5 (5.3)	18 (100.0)	0 (0)	2 (100.0)	0 (0)
Take of shoal and bull nets combined:													
9 inches	430	312	118	0 (0)	3 (100.0)	81 (47.9)	88 (52.1)	181 (87.4)	26 (12.6)	45 (97.8)	1 (2.2)	5 (100.0)	0 (0)
8½ inches	430	382	48	0 (0)	3 (100.0)	129 (76.3)	40 (23.7)	202 (97.6)	5 (2.4)	46 (100.0)	0 (0)	5 (100.0)	0 (0)

TABLE 27.—*Distribution by age groups of legal-sized yellow perch from gill nets, 1927–28 and 1943–48*

[Percentages in parentheses]

Year and minimum legal size	Total number	Number and percentage in age group—				
		I	II	III	IV	V
Period 1927–28:						
1927:						
9 inches	136	0 (0)	38 (27.9)	78 (57.4)	16 (11.8)	4 (2.9)
8½ inches	146	0 (0)	48 (32.9)	78 (53.4)	16 (11.0)	4 (2.7)
1928:						
9 inches	176	0 (0)	43 (24.4)	103 (58.5)	29 (16.5)	1 (0.6)
8½ inches	236	0 (0)	81 (34.3)	124 (52.6)	30 (12.7)	1 (0.4)
Total, 1927–28:						
9 inches	312	0 (0)	81 (26.0)	181 (58.0)	45 (14.4)	5 (1.6)
8½ inches	382	0 (0)	129 (33.8)	202 (52.9)	46 (12.0)	5 (1.3)
Average percentage: [1]						
9 inches		(0)	(26.1)	(58.0)	(14.1)	(1.8)
8½ inches		(0)	(33.6)	(53.0)	(11.8)	(1.6)
Period 1943–48:						
1943: 8½ inches	114	6 (5.3)	64 (56.1)	34 (29.8)	8 (7.0)	2 (1.8)
1944: 8½ inches	56	0 (0)	42 (75.0)	13 (23.2)	1 (1.8)	0 (0)
1945: 8½ inches	74	1 (1.3)	35 (47.3)	35 (47.3)	3 (4.1)	0 (0)
1946: 8½ inches	207	1 (0.5)	148 (71.5)	48 (23.2)	9 (4.3)	1 (0.5)
1947: 8½ inches	389	9 (2.3)	74 (19.0)	235 (60.4)	71 (18.3)	0 (0)
1948: 8½ inches	291	0 (0)	170 (58.4)	103 (35.4)	18 (6.2)	0 (0)
Total, 1943–48:						
8½ inches	1,131	17 (1.5)	533 (47.1)	468 (41.4)	110 (9.7)	3 (0.3)
Average percentage: [1]						
8½ inches		(1.6)	(54.5)	(36.5)	(7.0)	(0.4)
Total, all years [2]	1,443	17	614	649	155	8
Average percentage: [1]						
Effective limits		(1.2)	(47.4)	(41.9)	(8.8)	(0.7)
8½-inch limit		(1.2)	(49.3)	(40.6)	(8.2)	(0.7)

[1] Unweighted mean.
[2] Minimum legal size was 9 inches in 1927 and 1928 and 8½ inches in all later years.

yellow perch in impounding-net and gill-net collections. The small numbers of specimens do not warrant detailed comparisons of the remaining age groups. Attention should be called to the fact that in both 1927 and 1928 the samples taken by gill nets did not contain fish caught as late in the season as did those taken by impounding nets. Consequently, the yellow perch taken by gill nets may be expected to have completed less of the season's growth. Had the collections from both types of gear been made at the same time within the season, the advantage of the gill-net samples with respect to the percentage of legal-sized yellow perch in the age groups would probably have been even greater.

Differences in the age composition of collections from the two types of gill nets were not great, although there was a slight tendency for bull nets to take more of the younger fish (table 25). The only dominant group II occurred in the 1928 bull-net collection, and when the data for 1927 and 1928 are combined, bull nets may be seen to have taken relatively more fish of age group II than did shoal nets and relatively fewer of the older age groups. Likewise, the differences in the proportion of legal-sized yellow perch in corresponding age groups of shoal-net and bull-net collections were not large. The best represented age groups (II and III) of the shoal-net samples contained slightly higher percentages of legal-sized fish than the same age groups in bull-net samples.

The data on numerical and percentage age composition of the legal-sized yellow perch taken by gill nets are presented in table 27 with the catches of shoal and bull nets combined. Added to the 1927 and 1928 data are those obtained from samples of the commercial catch by gill nets in 1943–48. Age group III dominated the samples in both 1927 and 1928 and made up 58 percent of the total at the then-effective size limit of 9 inches (53 percent at the present 8½-inch size limit). Age groups II and IV made up 26.1 and 14.1 percent (33.6 and 11.8 percent at the 8½-inch limit) and formed the only other well-represented groups in the catches. Age group I was not represented at all. The 1943–48 data differed from those of the earlier years in that age-group-II fish dominated in 4 years, age groups II and III were equally represented in one, and age group III was dominant in only 1 year. The averages for the 6 years (comparable to the averages at the 8½-inch size limit in 1927–28) showed that group II made up 54.5 percent of the total, group III 36.5 percent, group IV 7 percent, and group I 1.6 percent. Thus it is seen that there was not only a shift in dominance from group III in 1927–28 to group II in 1943–48 but also an accompanying decrease in the relative abundance of the fish in groups IV and V and an increase in the number of those in group I.

Explanation of the difference in age composition of the legal-sized yellow perch taken by gill nets in 1927–28 and 1943–48 probably lies in the time of year the fish were captured. All of the 1927–28 samples were collected in July and August while those for 1943–48 were taken from late September to early November. The samples obtained in July and August (1927–28) unquestionably were made up of fish that had not completed the season's growth, whereas those taken later in the year (1943–48) could be expected to have

completed, or nearly completed, growth for the year. The continued growth, especially of the age group just entering the commercial fishery in large numbers (group II) can be expected to increase the relative abundance of the younger individuals among the legal-sized fish. The belief that the time of capture in a year explains the shift of dominance from group III to group II is supported by the strikingly similar changes found in the impounding-net data.

If the data for impounding and gill nets are considered together, it may be stated that the fishery is supported chiefly by age groups II and III. Age group III dominated the commercial catch of gill nets in late summer of both 1927 and 1928. The same age group is in all probability usually dominant in the early-season catches also. The late-season (late September to early November) commercial catches by gill nets were dominated by age group II in 4 of the 6 years 1943–48. Age group III dominated the late-season gill-net catches only once (1947) and age groups II and III were of equal abundance in 1945. The commercial catch of impounding nets appeared to be dominated by age group III in the spring and during at least part of the summer. As growth during the summer brings an increasing percentage of age group II to legal size this age group assumed a more important position in the catch. Dominance by age group II seems to be characteristic of late-season impounding-net catches, although there may be exceptions, as in 1929 and 1945, when age group III may be the stronger.

The dependence of the fishery on two age groups renders the abundance of the Lake Erie perch very sensitive to natural fluctuations in the strength of year classes and vulnerable to overfishing. The small quantity of fish of commercial size that is carried over from one year to the next makes the maintenance of protective measures to ensure an adequate stock of spawners at all times highly imperative.

The percentage representation of the year classes in each year's collection of yellow perch from impounding nets in Lake Erie is recorded in table 28. The data for the 1937 collection have been omitted because of the long time interval separating this sample from the earlier collections. Discussion of the year-class composition of the 1937 samples will be based on the age-composition data of table 21. No tabulation has been presented of the year-class composition of gill-net samples because of the highly selective action of that gear.

The inability of impounding nets to retain representative samples of the younger age groups, and the rapid rate at which year classes disappear from the fishery owing to the short life span, combine to make interpretation of data on the year-class composition of the samples most difficult. Age group 0 (first year of life) is of course absent from all collections, and normally group-I fish occur

TABLE 28.—*Occurrence of year classes of yellow perch in the catch of impounding nets of Lake Erie*

[Asterisk designates dominant year class each year; roman numerals show age at capture]

PART I—PERCENTAGE BASED ON ALL FISH TAKEN

Year of capture	Year class of—								
	1922	1923	1924	1925	1926	1927	1928	1929	1930
1927	0.4 V	1.0 IV	9.8 III	39.9 II	*48.9 I				
1928			.5 IV	7.6 III	*90.6 II	1.2 I			
1929			.3 V	5.3 V	*54.9 III	32.3 II	7.2 I		
1930					1.8 IV	20.3 III	*77.5 II	0.4 I	
1932							24.8 IV	*73.7 III	1.5 II

PART II—PERCENTAGE BASED ON COMMERCIAL CATCH

Year of capture	Year class of—								
	1939	1940	1941	1942	1943	1944	1945	1946	1947
1943	3.6 IV	17.9 III	*57.1 II	21.4 I					
1944			14.8 III	*85.2 II					
1945		1.3 V	12.4 IV	*55.6 III	30.7 II				
1946			.9 V	3.3 IV	23.5 III	*72.3 II			
1947				.9 V	6.0 IV	41.9 III	*50.9 II	0.3 I	
1948						3.1 IV	24.0 III	*71.2 II	1.7 I

only in small numbers. Age group II is affected less by the selective action of the gear although many fish of this age seem to be too small to be retained in the nets in spring and early summer (p. 221). It appears, then, that estimates of the relative abundance of the year classes of the Lake Erie perch must be based chiefly on the representation of the older fish in the different years' samples. The relative strength of age group II may be considered significant only if the sample was taken late in the season. The scarcity of group-I fish cannot be held to indicate a weak year class, although a great abundance of yellow perch of this age may be considered evidence of a strong one.

Ordinarily the estimate of the strength of a year class is based on a knowledge of its relative abundance in the collections of several successive years. In the Lake Erie yellow perch, however, the great scarcity of all fish older than age group III, together with the unreliability of data on the abundance of the younger age groups, makes the application of this method very difficult. Further complications arise from the failure to obtain data in 1938 and 1939, and the fact that only the legal-sized fish were sampled in 1943–48.

Because of the limitations just outlined it is not possible to make a precise arrangement of the year classes of the Lake Erie yellow perch in the order of their abundance. In fact it is possible to speak with certainty concerning only one of them—the year class of 1926. This year class was without doubt one of exceptional strength. It dominated the impounding-net collections of three successive years, 1927, 1928, and 1929. Dominance of this year class as group I and as group III is particularly significant. The only dominant group I of the collections occurred in the 1927 samples. In the remaining collections, age group I made up no more than 7.2 percent of the samples except in 1937 and 1943. Age group III was dominant in the late-season collections of both 1929 and 1945. It should be pointed out further than in 1928 the 1926 year class provided relatively the strongest group II in any of the collections (90.6 percent of the total).

Three other year classes appeared to have been of more than ordinary strength. The 1936 year class as group I made up 47.3 percent of the entire 1937 sample (table 21). The only other collection with such an abundance of group-I fish was made in 1927 when the 1926 year class dominated the catch of impounding nets. Unfortunately, no samples were obtained in either 1938 or 1939 and, as a consequence, nothing is known of the strength of the 1936 year class at the ages when they would contribute most to the fishery. However, production increased from 3,305,000 pounds in 1936 to 7,782,000 pounds in 1938 when the 1936 year class would have entered the commercial fishery in greatest numbers. A large increase in yield is to be expected when a strong year class enters the fishery, and the 236-percent increase from 1936 to 1938 in the catch of yellow perch may be taken as evidence, if not proof, that the 1936 year class was of more than ordinary strength. The sharp decline to 3,015,000 pounds in 1939 in the take of yellow perch could mean the exhaustion of an abundant year class by an intense fishery.

Despite the fact that the evaluation of the strength of year classes in the 1943–48 period is handicapped by lack of knowledge of the abundance of group-I fish in those years, it seems evident that the 1942 year class was one of considerable size. It comprised 21.4 percent of the 1943 samples as age group I. The same year class was strongly dominant as group-II fish in 1944 (85.2 percent) and continued to dominate the commercial samples as age group III in 1945 (55.6 percent). The strong representation of the 1942 year class as group-I fish in the commercial yield in 1943 and the dominance of the group in the two succeeding years could have been accomplished only by remarkably good survival.

Evidence, less convincing but nevertheless strongly suggestive, points to 1944 as having produced a year class that was stronger than that of either 1943 or 1945. The 1944 year class as group-II fish made up 72.3 percent of the 1946 commercial samples and contributed heavily (41.9 percent) to the 1947 take when they were in age group III.

The 1943–48 data from gill nets (table 27) provide some evidence of the relative strength of year classes despite the fact that these nets are highly selective and the samples were taken from the legal-sized yellow perch. Age group III made up 47.3 percent of the legal-sized fish in 1945 and equaled the abundance of group II. This high relative abundance of age group III supports the conclusion reached from the trap-net data that the 1942 year class was of more than ordinary

strength. Although the fish assigned to age group III dominated the late-season commercial catch of yellow perch by gill nets in 1947, the evidence that the 1944 year class was exceptionally strong is not conclusive. As group-II fish the 1944 year class strongly dominated (71.5 percent) the commercial catch in 1946 and exhibited the second-strongest dominance in the 6-year period 1943–48, but the class appeared sparingly (1.3 percent) as age group I in 1945. Data from the gill nets add strength to the suggestion based on trap-net catches that the year class of 1944 was stronger than that of either 1943 or 1945.

The occurrence of rather wide fluctuations in the abundance of year classes has been observed in a large number of species, both marine and fresh-water. Despite the extensive studies that have been made of the fluctuations in abundance of year classes, relatively little is known concerning the underlying causes. It is agreed rather generally, however, that the fluctuations "have their origin in certain conditions prevailing at a very early period in the life of the fish" (Hjort 1914). The belief is general also that fluctuations depend on variations in meteorological-hydrographical conditions, although biological conditions (for example, competition for food among the young and increase in predators) may at times be important.[13]

Under conditions of a stabilized fishing intensity, it is believed that the causes of fluctuations in the abundance of year classes in the fishes of Lake Erie are most probably to be found in the meteorological-hydrographical conditions. It is recognized that overfishing and other factors also may be involved. The simultaneous occurrence in 1926 of a strong year class in seven species strongly suggests that competition for food among the young is not normally a limiting factor. The comparatively low yield of the fishery in 1926, a year that produced a strong year class, indicates that as long as the population is maintained at a reasonable strength the number of spawners may not be the primary determining factor.

The weather records from the Sandusky, Ohio, station of the U. S. Weather Bureau (1919–48) have been examined in an effort to detect a possible correlation between weather conditions and the strength of the year classes. It has been assumed that conditions in 1926 and 1942 and probably in 1936 and 1944 were exceptional as those years produced the strongest year classes of yellow perch found within the data, and that the causes for the strength of those year classes should be found in the extent and manner in which the meteorological conditions of those years differed from other years. It was expected further that conditions would be more comparable in the years 1926 and 1942 than in any other years.

Because of the previously mentioned impossibility of evaluating accurately the strength of each year class it is possible to speak only in general terms concerning the effects of weather, hence detailed weather data will not be presented. The temperature data that were examined referred to air temperatures. As mentioned previously, trends in air temperature no doubt indicate approximate trends in water temperature, especially in such shallow water as is found in western Lake Erie. It was found that the winter of 1925–26 (November to February) was cold and that the following prespawning period (March and April) was the coldest for the years 1919 to 1948. However, both the winter of 1941–42 and the prespawning period in 1942 were warmer than average. The 2 years probably producing strong year classes (1936 and 1944) differed in that the winter of 1935–36 was exceptionally cold and that of 1943–44 was warmer than average. The prespawning period in 1936 had above average temperatures but in 1944 temperatures were below average. In other months of the year temperature exhibited no relation to the strength of the year classes.

Although all of the 4 years that apparently produced strong year classes had less than average rainfall in May and June, the total precipitation in both 1942 and 1944 was only slightly below normal and amounted to between two and three times that in either 1926 or 1936. Wind velocities and percentage of possible sunshine appear to bear even less relation to the strength of year classes than the other factors considered. Van Oosten (1948) pointed out that there was no relation between turbidity and strength of year classes.

The contradictory evidence of the effects of temperature during the winter and prespawning period and total precipitation during May and June on the strength of year classes makes it appear that no simple relation exists. Although

[13] Jensen (1933) gave a detailed review of the literature and a critical discussion of the causes of fluctuations in the abundance of marine fish of the North Sea and neighboring waters.

extremely high or low temperatures and severe storms may lead to catastrophic destruction of eggs and small fish, the strength of a year class is believed to depend normally on the sum of the effects of many factors. It seems entirely reasonable to suppose that the controlling factors have to do with the coincidental occurrence of early feeding by the newly hatched fish and the appearance of suitable food organisms in adequate amounts.

LENGTH-WEIGHT RELATION

The mathematical relation between length and weight of the yellow perch of Lake Erie in 1927–37 was determined by fitting the equation $W=cL^n$ to the average empirical length and weight of each 5-mm. standard-length frequency interval over the range 106 to 250 mm. (5.0 to 11.4 inches total length). Length intervals both longer and shorter than this range contained less than 28 fish each and were not employed in the fitting of the equation because of possibly unreliable averages. The data represent all yellow perch with standard lengths of 106 to 250 mm. that were measured and weighed without regard for locality, sex, season and year of capture, or gear employed. Data on the length and weight of Lake Erie yellow perch in 1943–48 are not included because analysis of these later data showed them to be similar in every respect to those obtained during the earlier years. The equation derived from the 1927–37 data applied equally well to the 1943–48 material.

The equation that best describes the length-weight relation of the Lake Erie yellow perch is:

$$W=1.766\times10^{-5}L^{3.015},$$

in which W=weight in grams, and L=standard length in millimeters. Since n=3.015, it may be said that the weight of the yellow perch in Lake Erie increased approximately as the cube of the length (n=3.0).

Table 29 shows the actual and calculated weights for each 5-mm. interval of standard length of the yellow perch of Lake Erie from 1927 to 1937. Weights were computed both from the cube relationship and from the more general equation ($W=cL^n$). It was found that weights calculated by the general equation agreed closely with those computed by the equation $W=1.91\times10^{-5}L^3$. (The weighted grand average K for all Lake Erie yellow perch was 1.91.) Weights calculated by the two equations were in complete agreement for all but 6 of the 31 frequency intervals for fish with standard lengths of less than 236 mm., and in no interval differed by more than 1 gram. The weights computed by the two equations agreed at no lengths greater than 235 mm. The weights of these larger yellow perch calculated from the cubic relationship were always less than those computed from the more general equation but at no length was the difference between the two calculated weights greater than 4 grams. It is true also that the differences between the two corresponding calculated weights tended to increase progressively as

TABLE 29.—*Actual and calculated weights of Lake Erie yellow perch by 5-millimeter length intervals*

[Data based on all fish weighed during the investigation]

Standard-length interval [1]	Total length	Number of fish	Average actual weight	Average weight calculated from equation—	
				$W=cL^n$	$W=K\times10^{-5}L^3$
	Inches		*Grams*	*Grams*	*Grams*
83 mm	3.9	1	7	11	11
88 mm	4.1			13	13
93 mm	4.4	1	21	15	15
98 mm	4.6	1	21	18	18
103 mm	4.8	8	21	21	21
108 mm	5.1	28	24	24	24
113 mm	5.3	52	26	27	28
118 mm	5.5	53	29	31	31
123 mm	5.8	58	35	35	36
128 mm	6.0	76	40	40	40
133 mm	6.2	93	45	45	45
138 mm	6.4	144	51	50	50
143 mm	6.6	281	58	56	56
148 mm	6.8	431	64	62	62
153 mm	7.1	513	69	68	68
158 mm	7.3	751	77	75	75
163 mm	7.5	992	83	82	83
168 mm	7.8	1,161	91	90	91
173 mm	8.0	1,275	98	99	99
178 mm	8.2	1,463	108	108	108
183 mm	8.5	1,633	117	116	117
188 mm	8.7	1,844	126	127	127
193 mm	8.9	1,997	137	137	137
198 mm	9.1	2,252	149	148	148
203 mm	9.3	2,124	162	160	160
208 mm	9.5	1,845	174	172	172
213 mm	9.8	1,531	186	185	185
218 mm	10.0	1,066	200	198	198
223 mm	10.2	681	213	212	212
228 mm	10.4	399	227	227	226
233 mm	10.6	166	240	242	242
238 mm	10.8	113	255	258	257
243 mm	11.1	66	266	275	274
248 mm	11.3	34	282	292	291
253 mm	11.5	5	304	310	309
258 mm	11.7	7	334	329	328
263 mm	12.0	1	312	349	347
268 mm	12.2	5	349	369	368
273 mm	12.4	1	404	390	389
278 mm	12.6			412	410
283 mm	12.9	3	418	435	433
288 mm	13.1	2	524	459	456
293 mm	13.3			483	480
298 mm	13.6	1	475	508	505
303 mm	13.8			535	531
308 mm	14.0			562	558

[1] In 5-mm. intervals.

the standard length of the fish increased above 270 mm.

A comparison of the average actual weights with the calculated weights shows that there was excellent agreement over most of the length range for which there were large numbers of fish.[14] Over the standard length range of 103 to 238 mm. the actual weights at no point disagreed with either of the computed weights by more than 3 grams. It is apparent also that calculated weights obtained by the two equations agreed almost equally well with the average actual weights over this length range. The lack of agreement between the observed weights and the computed weights of perch with standard lengths less than 103 mm. may be due to the small number of specimens of that size. The empirical weights were somewhat less than either calculated weight at all but three of the lengths greater than 238 mm. (intervals with midpoints at 258, 273, and 288 were the exceptions). Over this range, the weights calculated on the basis of the cubic relationship were ordinarily closer to the observed weights than were those calculated from the more general equation. The fact that the actual weights of the larger fish were usually less than the computed weights may indicate that both equations fail to fit the data exactly for standard lengths greater than 238 mm., or it may be due to the small number of individuals in most of the frequency intervals. Another possible explanation of the lower actual weights at lengths greater than 238 mm. is that the gill nets selected only the lighter of the longer fish.

[14] The average actual weights are the averages of all fish in each 5-mm. interval. Only the midlength of each interval is shown in the table.

The weights calculated from the length-weight equation, $W=1.766\times10^{-5}L^{3.015}$, are shown graphically in figure 10. The use of two scales permits ready conversion from metric to English units of weights and measures. The factors needed most frequently for conversions between standard, fork, and total lengths are shown in table 30. It was mentioned (p. 252) that intervals of standard length that contained less than 28 fish were not used in the determination of the general length-weight equation. Hence, the points on the curve that lie below 106 mm. and above 250 mm. are outside the range to which the curve was actually fitted. However, the closeness with which the extrapolated portions of the curve (shown by broken lines) fit the average actual weights based on few specimens indicates that, in spite of the discrepancies already mentioned, the curve is for practical purposes applicable to the length-weight relation over the entire range represented.

COEFFICIENT OF CONDITION (*K*)

The condition of fishes and fluctuations in the values of the coefficient of condition (*K*) involve problems that are distinctly different from the description of the general length-weight relation (see Hile 1936, for detailed discussion). Condition, or relative heaviness, is influenced by those physiological and environmental factors that affect the general well-being of the individuals. The present data permit a description of the fluc-

TABLE 30.—*Factors for conversions between standard, fork, and total lengths of Lake Erie yellow perch*

[Number of specimens employed to determine values of the factors are shown in parentheses]

Conversion of—	Factors to be employed for standard lengths of—				
	80 mm. and under	81 to 130 mm.	131 to 190 mm.	191 to 220 mm.	221 mm. and over
Standard length to total length (same unit of measurement)	1.215	1.193	1.174	1.165	1.156
	(87)	(112)	(648)	(1,267)	(513)
Standard length in millimeters to total length in inches	.0478	.0470	.0462	.0459	.0455
	(87)	(112)	(648)	(1,267)	(513)
Standard length to fork length (same unit of measurement)		1.141	1.132	1.125	1.119
	(0)	(5)	(285)	(591)	(131)
Standard length in millimeters to fork length in inches		.0449	.0446	.0443	.0441
	(0)	(5)	(285)	(591)	(131)
Total length to standard length (same unit of measurement)	.823	.838	.852	.858	.865
	(87)	(112)	(648)	(1,267)	(513)
Total length in inches to standard length in millimeters	20.904	21.285	21.641	21.793	21.971
	(87)	(112)	(648)	(1,267)	(513)
Total length to fork length (same unit of measurement)		.956	.964	.966	.968
	(0)	(5)	(285)	(591)	(131)
Fork length to standard length (same unit of measurement)		.876	.883	.889	.894
	(0)	(5)	(285)	(591)	(131)
Fork length in inches to standard length in millimeters		22.250	22.428	22.581	22.708
	(0)	(5)	(285)	(591)	(131)
Fork length to total length (same unit of measurement)		1.046	1.037	1.035	1.033
	(0)	(5)	(285)	(591)	(131)

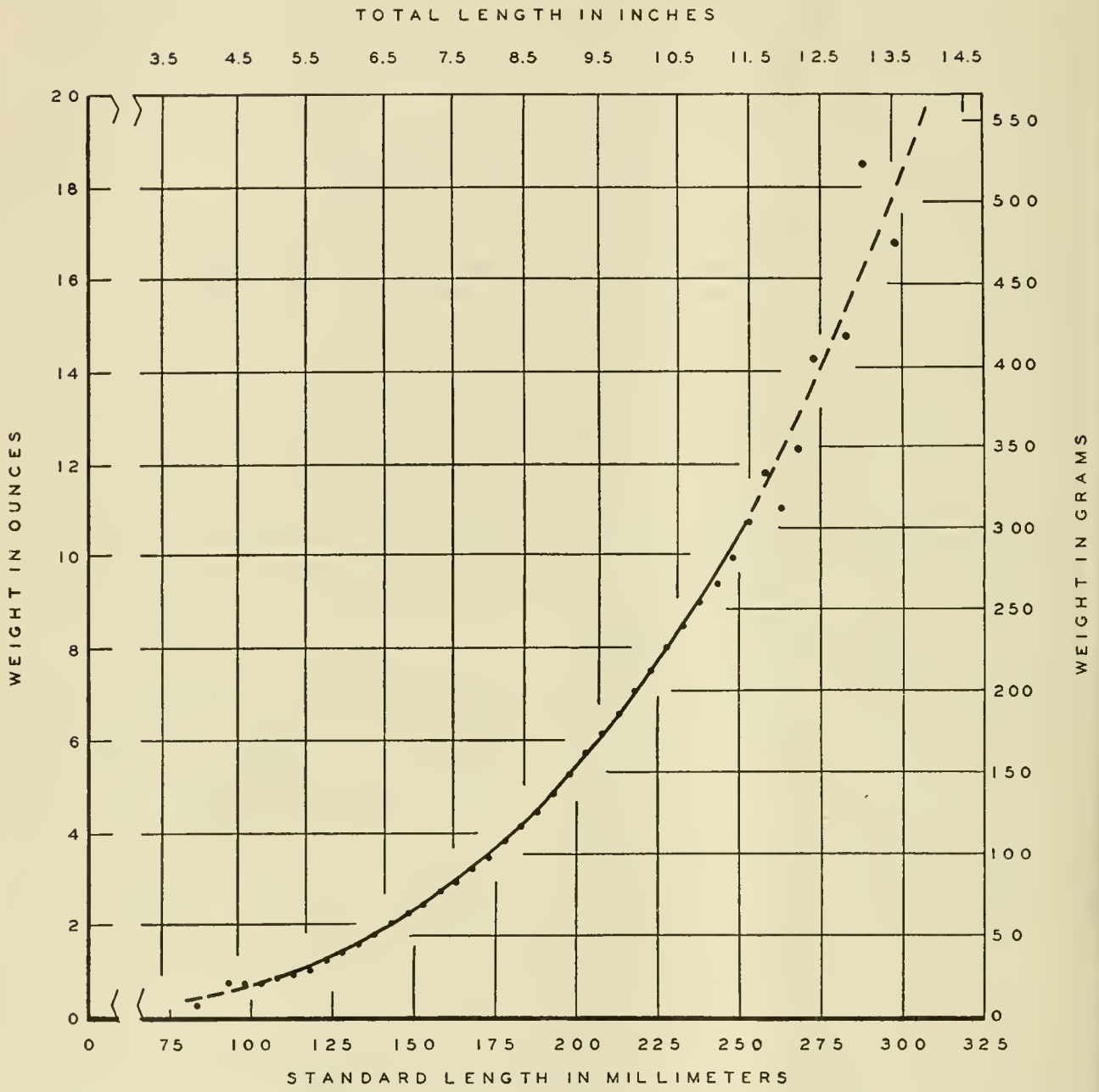

FIGURE 10.—Relation between length and weight in yellow perch of Lake Erie. Solid portion of the curve represents length range to which equation $W=cL^n$ was fitted; broken lines represent the curve in length ranges not well represented in the data. Dots show averages of empirical data grouped into 5-mm. length intervals.

tuations in the coefficient of condition (K) of the Lake Erie yellow perch according to month of capture, sex and maturity, state of gonads, age, length, and type of gear employed. The data obtained from samples taken in the period 1943–48 will be omitted from this discussion since they contribute nothing new and would bring about no important changes in the conclusions.

Monthly and annual fluctuations in the value of K

Among the factors that might be expected to influence monthly variations in K are food, degree of activity, and stage of sexual maturity. Spawning, and the preparatory sexual development, may be expected to produce the greatest changes in condition. Description of the monthly and annual fluctuations in the value of K in the Lake

Erie yellow perch is based entirely on specimens taken from impounding nets since, as will be shown later (p. 258), the type of gear employed influences the average value of K and gill nets are particularly selective in this respect.

Sex and stage of maturity were shown by separate analyses to have had very little effect on the value of K except in the spawning period. The data in table 31 showing the monthly fluctuations in condition of Lake Erie yellow perch according to year of capture therefore, include individuals for which sex or stage of maturity was not recorded. The data from samples obtained during April 1932, October 1934, and November 1937 are not shown in the table because each of those years was represented by only 1 month. The values of K for these 3 months were 2.24 (133 fish), 2.24 (207 fish), and 2.18 (131 fish), respectively.

Annual fluctuations in condition and differences with respect to the months represented in the various years' collections place limitations on the conclusions to be drawn from the data of table 31. Nevertheless, certain trends can be detected. It is obvious, for example, that perch tend to be in better condition in midsummer and late summer than in June. This is brought out by the following tabulation of the unweighted averages of K for corresponding months of 1928 and 1929:

	Average K		*Average* K
June	1.80	September	1.96
July	1.97	October	1.92
August	1.98	November	1.87

The monthly averages for the 2 years show a great improvement in condition from June to July. Condition remained good in August and September. The average K decreased slightly in September and underwent a greater decrease in October and November. The averages in table 31 show that the October-November decline was much more pronounced in 1929 than in 1928.

The averages for September, October, and November, 1927, suggest that loss of condition in the autumn may not be typical for the Lake Erie perch. In 1927 the value of K increased in both October and November. The averages for the 1930 collection, on the other hand, agreed with the trend of the 1928–29 averages. In 1930 the value of K increased markedly in July and remained at a high level in August and September. The only available comparisons of the averages of K for November and December (1929) indicate an improvement in condition in the latter month. Three comparisons are available of condition in May and June and one of condition in April and May. However, the possible disturbing effects of variations in the relative abundance of gravid and spent fish in the various April and May collections make it inadvisable to draw conclusions concerning monthly changes in condition from April to May and from May to June.

TABLE 31.—*Monthly values of* K *(condition) of Lake Erie yellow perch taken in impaunding nets, 1927–30*

Month	1927		1928		1929		1930	
	Number of specimens	Average value of K	Number of specimens	Average value of K	Number of specimens	Average value of K	Number of specimens	Average value of K
April	------	------	429	1.78	------	------	------	------
May	------	------	664	1.76	3,122	1.84	41	1.85
June	------	------	504	1.81	1,841	1.78	5	1.81
July	------	------	132	2.06	2,747	1.88	173	2.31
August	------	------	510	2.04	1,820	1.92	25	2.34
September	125	1.87	162	2.00	451	1.93	25	2.33
October	895	1.91	458	1.99	126	1.86	------	------
November	496	2.01	264	1.96	691	1.78	------	------
December	------	------	------	------	417	1.88	------	------
Average, all months	1,516	1.94	3,123	1.89	11,215	1.85	269	2.24
Average, excluding April and May	1,516	1.94	2,030	1.96	8,093	1.86	228	2.30

The grand averages for K in the different years' collections are not strictly comparable because of differences from year to year in the months represented. A more reliable estimate of the annual fluctuations in condition may be had from comparisons of averages for corresponding months. Comparisons of the averages for September, October, and November indicate that condition was slightly better in 1928 than in 1927. The large 1928 advantages in September and October overshadowed the 1927 advantage in November. Condition was poorer in 1929 than in 1928. The K averages were lower in 1929 in every month except May. The condition of the Lake Erie perch in 1929 was also probably poorer than in 1927. The September average was higher in 1929 than in 1927, but the October and November averages were both higher in 1927. The best condition of the 4 years occurred in 1930. With the exception of June which had the same K averages in 1928 and 1930, the monthly averages in 1930 were consistently greater than the corresponding averages in any other year. From the data just discussed it would appear that the probable order of the 4 years with respect to condition of the Lake Erie yellow perch from

best to poorest condition is: 1930, 1928, 1927, and 1929.

The K averages of 2.24 in April 1932 and October 1934, and 2.18 in November 1937 (p. 255), suggest that the condition of the Lake Erie yellow perch in these 3 years was excellent—probably superior to that in 1927, 1928, and 1929.

Fluctuations in value of K with stage of maturity

Great differences in value of K associated with stage of maturity were found in the comparison of the gravid and spent females taken in May. (Unfortunately, gravid and spent males were not recorded separately in the field records.) The detailed information on the loss of weight by the females at spawning is presented in table 32 where the data have been arranged to show the average weight in grams and the average K before and after spawning for each 5-mm. standard-length interval. For both gravid and spent females the changes of K with increase in length appeared to be random rather than to exhibit a progressive increase or decrease. Consequently, there was no obvious relation between the percentage loss of weight and the length of the specimens. The loss of weight varied from 3.4 to 24.6 percent. The average of the percentages computed from the best-represented intervals, those in which both gravid and spent fish were represented by seven or more specimens, showed a weight loss of 16.1 percent at spawning. A slightly lower estimated loss of weight (15.5 percent) was obtained from the weighted-average coefficient of condition.

Fluctuations in value of K with age

Data for the study of the variations of K with age are given in table 33. To avoid the distorting effects of monthly and annual variations in condition, averages are given for each month's collection of each year. Since sex and stage of maturity have little influence on the value of K in the summer and autumn, the data include all the fish whose ages were determined. The data of table 33 do not point toward any dependence of condition on age. It is true that in 7 of 10 comparisons fish of age group II had lower average coefficients of condition than those of age group I. This difference can be explained, however, as the result of gear selectivity. Since the group-I fish were near the smallest size that could be retained by the impounding nets it is readily conceivable that only the heavier individuals of that age group were retained. There is less indication that gear selectivity affected the K values of age groups II and III although numbers of the group-II yellow perch were below the theoretical maximum length of escape (170 mm.). Gear selection possibly may account for the fact that group II had the larger average K in 9 of 10 comparisons for months earlier than October (see p. 221). In the later months, after group II has practically completed the third season of growth, age group III had the higher K values in all 7 comparisons (October, November, and December). Comparisons of age groups III and IV reveal that the former had the higher average K 6 times whereas the latter had the higher value 2 times. The two age groups

TABLE 32.—*Comparison of average weights and condition* (K) *of gravid and spent female yellow perch taken by impounding nets in Lake Erie, May 1929*

[Number of specimens in parentheses]

Standard-length interval	Average total length	Gravid females		Spent females		Loss of weight at spawning
		Average weight	K	Average weight	K	
	Inches	*Grams*		*Grams*		*Percent*
166 to 170 mm	7.8	89 (3)	1.89	86 (10)	1.82	3.4
171 to 175 mm	8.0	122 (5)	2.36	92 (20)	1.78	24.6
176 to 180 mm	8.2	115 (10)	2.05	99 (24)	1.75	13.9
181 to 185 mm	8.5	128 (29)	2.08	109 (52)	1.77	14.8
186 to 190 mm	8.7	138 (58)	2.08	118 (75)	1.78	14.5
191 to 195 mm	8.9	148 (82)	2.06	125 (101)	1.74	15.5
196 to 200 mm	9.1	161 (90)	2.08	135 (107)	1.74	16.2
201 to 205 mm	9.3	172 (100)	2.05	147 (92)	1.76	14.5
206 to 210 mm	9.5	186 (90)	2.06	157 (77)	1.75	15.6
211 to 215 mm	9.8	200 (40)	2.07	167 (48)	1.73	16.5
216 to 220 mm	10.0	211 (42)	2.04	175 (39)	1.69	17.1
221 to 225 mm	10.2	232 (26)	2.09	181 (7)	1.63	22.0
226 to 230 mm	10.4	246 (14)	2.08	214 (5)	1.81	13.0
231 to 235 mm	10.6	261 (6)	2.06	232 (3)	1.83	11.1
236 to 240 mm	10.8	291 (1)	2.16	230 (4)	1.71	20.7
Weighted average K			2.07 (596)		1.75 (664)	
Average loss in weight [1]						16.1

[1] Unweighted mean, based on those length intervals in which both gravid and spent fish are represented by at least 7 individuals.

had the same values in November 1927. Only three comparisons were available between age groups IV and V, and in each the older age group had the lower K. In general, fluctuations of K with age may be considered random among all age groups in which gear selectivity is absent or unimportant, although there was a tendency for a progressive decrease with age during the period April to September. It may be justified to conclude, however, that generally condition is independent of age in the Lake Erie yellow perch. No computation was made of average values of K for all data combined since the combined effects of monthly variations and of variations in the numbers of specimens would cause these averages to be of little significance.

TABLE 33.—*Coefficient of condition* (K) *of Lake Erie yellow perch according to age, month, and year of capture*

[Number of specimens in parentheses]

Month and year	Age group				
	I	II	III	IV	V
April: 1932		2.35 (2)	2.26 (98)	2.23 (33)	
July:					
1928		2.05 (107)	1.85 (21)	1.93 (4)	
1929		2.00 (13)	1.90 (131)	1.82 (16)	1.72 (1)
1930		2.51 (128)	2.16 (40)	2.13 (4)	
August:					
1928	2.61 (7)	2.07 (393)	2.14 (14)		
1929	2.05 (7)	1.91 (29)	1.86 (32)		
1930		2.32 (23)	2.14 (2)		
September:					
1928		2.00 (148)	1.94 (10)		
1929	2.01 (6)	2.16 (22)	2.05 (136)		
1930	2.38 (1)	2.41 (21)	2.12 (3)		
October:					
1927	1.90 (74)	1.89 (61)	1.93 (28)	1.96 (4)	1.91 (2)
1928		1.96 (61)	2.05 (9)	2.02 (1)	
November:					
1927	2.01 (161)	1.92 (129)	2.08 (19)	2.08 (1)	
1928	1.99 (4)	1.99 (123)	2.02 (16)		
1929	1.87 (28)	1.79 (179)	1.84 (218)	1.80 (33)	1.78 (2)
1937	2.30 (62)	2.07 (66)	2.15 (3)		
December: 1929	1.93 (42)	1.91 (138)	1.94 (115)	1.93 (12)	

The range of fluctuation of K for the age groups of Lake Erie yellow perch extended from 1.72 to 2.61. The individual yellow perch were found to have values of K ranging from 1.13 to 3.23, with the average 1.91. Comparisons of these values of K with those found in other waters of the Great Lakes reveal that the yellow perch of Lake Erie were a little heavier than the ones in Saginaw Bay (Hile and Jobes 1941), about equal to those in Green Bay, and somewhat more slender than the yellow perch in northwestern Lake Michigan (Hile and Jobes 1942).

Influence of rate of growth on value of K

The possibility that the values of K of the age groups were influenced by varying proportions of faster or slower growing individuals has been investigated. Table 34 permits comparisons of K for yellow perch of the same length but of different ages and for fish of different lengths but of the same age. All comparisons have been limited to fish collected in the same year and month. The data have been limited further to the 1927 and 1929 collections from trap nets since those collections had the most suitable distribution of the age groups, that is, contained adequate samples from more than one age group. It may be seen that there were no consistent differences between the values of K for fish of the same length but different age. In other words, neither the older (slow growing) nor the younger (rapid growing) yellow perch maintained a consistent advantage. This indication that individual growth rate did not influence individual condition is supported by the fact that the longer (more rapid growing) indi-

TABLE 34.—*Comparison of condition* (K) *in Lake Erie yellow perch at different ages and lengths taken by trap nets*

[Number of specimens in parentheses]

Standard-length interval	Average total length	Value of K in—							
		October 1927		November 1927		November 1929		December 1929	
		I	II	I	II	II	III	II	III
	Inches								
121 to 130 mm	5.9		1.67 (1)	1.96 (1)	3.23 (1)				
131 to 140 mm	6.3	1.71 (4)		1.98 (6)					
141 to 150 mm	6.7	1.79 (7)	1.71 (3)	2.02 (27)	2.03 (5)	1.83 (2)		1.93 (2)	
151 to 160 mm	7.2	1.95 (17)	1.96 (3)	1.99 (31)	1.95 (9)	1.81 (9)		1.85 (11)	
161 to 170 mm	7.6	1.87 (25)	1.91 (12)	2.01 (59)	1.97 (16)	1.70 (19)	1.73 (1)	1.86 (21)	2.02 (1)
171 to 180 mm	8.1	1.87 (16)	1.82 (10)	1.96 (34)	2.00 (38)	1.76 (23)	1.70 (4)	1.87 (30)	1.87 (11)
181 to 190 mm	8.6	1.80 (5)	1.88 (14)	1.91 (2)	1.99 (33)	1.76 (42)	1.72 (13)	1.88 (29)	1.83 (14)
191 to 200 mm	9.0		1.81 (11)	1.94 (1)	2.04 (17)	1.75 (43)	1.73 (34)	1.81 (18)	1.86 (21)
201 to 210 mm	9.4		1.85 (6)		2.01 (8)	1.73 (24)	1.78 (52)	1.85 (19)	1.88 (25)
211 to 220 mm	9.9		1.81 (1)		2.02 (4)	1.81 (8)	1.78 (48)	1.85 (7)	1.93 (23)
221 to 230 mm	10.3						1.83 (36)	1.76 (1)	1.93 (15)
231 to 240 mm	10.7						1.87 (18)		2.01 (5)
241 to 250 mm	11.2						1.93 (10)		
251 to 260 mm	11.6						1.78 (2)		

viduals of an age group did not differ in condition from the shorter, slower-growing fish of the same group.

The conclusion concerning the independence of growth rate and condition disagrees with Van Oosten's (1937) observation that the slower-growing individuals of the Lake Superior longjaw (*Leucichthys zenithicus*) were in the better condition. The same author (Van Oosten 1938) found, however, that growth rate and condition were not correlated in the Lake Erie sheepshead (*Aplodinotus grunniens*).

Effect of type of gear on determining value of *K*

The study of condition in the preceding sections was confined entirely to data from collections taken by trap and pound nets. Gill-net samples were excluded because of the effect of the selective action of that gear on the determination of K. The extent to which gill-net selection affects the determination of the value of the coefficient of condition may be seen from the data of table 35 which show the average K for each centimeter-length interval of the Lake Erie yellow perch taken from trap and gill nets in the same month and calendar year. Only five series were available for comparisons. The consistency with which the value of K was greater for fish caught in gill nets than in trap nets each month leaves little doubt that gill nets capture relatively heavier yellow perch than do impounding nets. In no single month did yellow perch taken in trap nets have average coefficients of condition as great as those of fish taken in gill nets.

The unweighted averages given in the two columns at the extreme right of table 35 give further information on the general influence of the type of net on the value of K. These averages were computed only for those lengths that were represented in the samples in all the months for which comparisons are given. An examination reveals that fish taken in gill nets had consistently higher average values of K. The averages also reveal a difference between gill- and trap-net samples with respect to the variation of K with length. Except for the relatively high figures at 141 to 150 mm. and 161 to 170 mm., the values of K tended to be constant at all lengths in the trap-net samples. The cause of the high values of K in these shorter fish taken in impounding nets has been discussed previously (p. 256). The nearly constant value of K over the interval 171 to 220 mm. is probably descriptive of true condition in the population. In the gill-net samples, on the contrary, K decreased consistently with each increase in length over the entire interval of 171 to 240 mm. In other words, the gill nets selected the heavier short fish and the slenderer long fish. At lengths below 171 mm. the captures of perch by gill nets were probably in large measure "accidents," that is, the fish were tangled in the meshes by their fins or the marginal bones of the mouth. The selective action of gill nets with

TABLE 35.—*Effect of type of gear on determination of the coefficient of condition* (K) *in Lake Erie yellow perch*

[Number of specimens in parentheses]

Standard-length interval	Average total length	September 1927		October 1927		July 1928		August 1928		November 1928		Average[1] K	
		Trap nets	Gill nets	Trap nets	Gill nets	Trap nets	Gill nets	Trap nets	Gill nets	Trap nets	Gill nets	Trap nets	Gill nets
	Inches												
91 to 100 mm.	4.5						2.23 (1)						
101 to 110 mm.	5.0							2.78 (1)					
111 to 120 mm.	5.4							2.86 (3)	2.13 (1)				
121 to 130 mm.	5.9	1.96 (3)	1.67 (4)	2.31 (1)				2.53 (2)					
131 to 140 mm.	6.3	1.90 (2)	1.90 (5)	1.70 (16)	1.90 (1)		2.70 (1)	2.72 (1)			1.90 (1)		
141 to 150 mm.	6.7	1.76 (1)	1.86 (9)	1.87 (38)	1.95 (2)	2.36 (5)	2.30 (8)	2.11 (12)	2.08 (2)	1.97 (2)	1.97 (1)	2.01	2.03
151 to 160 mm.	7.2	1.80 (1)	1.97 (7)	1.95 (67)	1.98 (1)	2.22 (18)	2.14 (13)	2.10 (65)	2.04 (3)		1.79 (1)		
161 to 170 mm.	7.6	1.76 (7)	1.80 (1)	1.93 (98)	2.00 (3)	2.14 (25)	2.16 (24)	2.04 (123)	2.19 (20)	2.12 (2)	2.12 (1)	2.00	2.05
171 to 180 mm.	8.1	1.89 (19)	2.64 (1)	1.91 (115)	2.02 (2)	1.98 (33)	2.11 (32)	2.01 (146)	2.19 (70)	2.00 (17)	1.94 (5)	1.96	2.18
181 to 190 mm.	8.6	1.82 (23)	2.16 (6)	1.90 (132)	2.16 (2)	2.06 (32)	2.18 (51)	2.03 (99)	2.18 (209)	1.99 (35)	2.10 (11)	1.93	2.16
191 to 200 mm.	9.0	1.93 (22)	2.05 (39)	1.90 (153)	2.02 (11)	1.90 (10)	2.17 (74)	2.00 (42)	2.14 (499)	1.98 (43)	2.09 (52)	1.94	2.09
201 to 210 mm.	9.4	1.88 (21)	2.05 (168)	1.91 (140)	2.08 (29)	1.50 (4)	2.06 (79)	1.97 (9)	2.08 (468)	1.96 (27)	2.05 (116)	1.94	2.06
211 to 220 mm.	9.9	1.88 (13)	2.00 (261)	1.94 (71)	1.97 (51)	1.94 (2)	2.02 (49)	2.01 (3)	2.01 (212)	1.96 (15)	1.95 (101)	1.95	1.99
221 to 230 mm.	10.3	1.87 (12)	1.99 (99)	1.94 (49)	1.96 (32)		1.91 (24)	2.11 (2)	1.96 (43)	1.89 (2)	1.91 (59)		1.95
231 to 240 mm.	10.7	1.92 (3)	1.91 (20)	1.92 (4)	1.83 (5)		1.86 (9)	1.68 (1)	1.91 (11)	2.25 (1)	1.88 (10)		1.88
241 to 250 mm.	11.2	1.73 (1)	1.85 (6)	1.90 (5)	1.90 (4)		1.68 (3)		1.78 (4)				
251 to 260 mm.	11.6			1.96 (2)			1.94 (1)	2.06 (1)					
261 to 270 mm.	12.1												
271 to 280 mm.	12.5				1.99 (1)								
Average[2]		1.87 (125)	2.01 (625)	1.91 (894)	1.99 (145)	2.06 (129)	2.10 (369)	2.04 (510)	2.10 (1,542)	1.98 (144)	2.00 (358)	1.96	2.04

[1] Unweighted mean, computed only for length intervals that were represented in all samples.
[2] Unweighted mean.

respect to condition would not be expected to operate on these accidental captures. The selection by gill nets of yellow perch according to the condition of the fish is similar to the action of drift (gill) nets on marine herring (Farran 1936) and supports the previous conclusion of a like action among the smaller perch by impounding nets.

From the preceding discussion it appears not only that gill nets tend to take relatively heavier yellow perch in Lake Erie than trap nets but that in gill-net samples K decreased with increases in length. The resulting distortion of the data justifies the exclusion of gill-net material from the study of condition.

SIZE AT MATURITY

A knowledge of size at sexual maturity has its practical application in the determination of the minimum legal size that may be needed to protect an adequate spawning stock. Data on the relation between total length and the percentage of maturity of the yellow perch taken in 1927–37 are given for the sexes separately and combined in table 36. The males matured at a much smaller size than the females: 47.4 percent of the males were mature or maturing at 6 to 6.5 inches and 48.4 percent of the females were mature or maturing at 8 to 8.5 inches. Any minimum legal size for the Lake Erie yellow perch, therefore, must be based on the maturity of females.

The shortest ½-inch total-length interval that contained a large percentage of mature females was 8 to 8.5 inches. At that length 48.4 percent were mature. At lengths of 8.5 to 9 inches 86.1 percent were mature, and at 9 to 9.5 inches 97 percent were mature. All females 9.5 inches and longer were mature. These data show that 86.1 percent of the females were mature in the shortest ½-inch total-length interval (8.5 to 9) available to the commercial fishery operating under the 8½-inch minimum legal size now effective in the Michigan and Ohio waters of Lake Erie (no size limit on yellow perch in Pennsylvania and New York waters). The samples collected in 1947–48 showed an even greater proportion of mature female yellow perch since 51 of 53 individuals (96.2 percent) in the 8.5- to- 9-inch interval were mature.

On the basis of the data in table 36 it is apparent that the great majority of female yellow perch in Lake Erie mature at total lengths between 8 and 9 inches. Reference to table 19 reveals that most of the fish with these lengths belonged to age group II (174 mm. standard length is equivalent to 8 inches total length, and 196 mm. equals 9 inches). It thereby becomes apparent that the majority of the female yellow perch reach maturity in Lake Erie during their third year of life and spawn for the first time early in their fourth year (as age-group-III fish). The average calculated length of the females at the end of the third year of life was 8.6 inches (table 7).

Although the data in tables 36 and 19 are from fish taken late in the fall one would expect little, if any, growth in winter or until spawning time in the spring. The percentages of maturity at the different sizes determined from fall samples, therefore, may be applied reasonably well to the spawning-season population. The small sample

TABLE 36.—*Relation between length of Lake Erie yellow perch and proportion of mature individuals, 1927–37*

Total-length interval [1]	Fork-length interval [1]	Standard-length interval	Sexes combined			Female			Male		
			Number mature	Number immature	Percentage mature	Number mature	Number immature	Percentage mature	Number mature	Number immature	Percentage mature
Less than 6.0 inches	Less than 5.7 inches	Less than 127 mm	0	38	0	0	15	0	0	23	0
6.0 to 6.5 inches	5.7 to 6.3 inches	127 to 140 mm	10	17	37.0	1	7	12.5	9	10	47.4
6.5 to 7.0 inches	6.3 to 6.7 inches	141 to 149 mm	26	50	34.2	0	31	0	26	19	57.8
7.0 to 7.5 inches	6.7 to 7.2 inches	150 to 161 mm	82	154	34.7	7	95	6.9	75	59	56.0
7.5 to 8.0 inches	7.2 to 7.7 inches	162 to 172 mm	216	189	53.3	30	131	18.6	186	58	76.2
8.0 to 8.5 inches	7.7 to 8.2 inches	173 to 183 mm	521	137	79.2	103	110	48.4	418	27	93.9
8.5 to 9.0 inches	8.2 to 8.7 inches	184 to 195 mm	901	64	93.4	348	56	86.1	553	8	98.6
9.0 to 9.5 inches	8.7 to 9.2 inches	196 to 206 mm	737	15	98.0	423	13	97.0	314	2	99.4
9.5 to 10.0 inches	9.2 to 9.7 inches	207 to 218 mm	426	0	100.0	290	0	100.0	136	0	100.0
10.0 inches and over	9.7 inches and over	219 mm. and over	236	0	100.0	190	0	100.0	46	0	100.0

[1] Fish included within each total-length and fork-length interval had lengths equal to the lowest and up to, but not including, the greatest length of the interval.

obtained during the breeding season suggests that spawning in itself may protect immature females since only 3 of 27 females (11.1 percent) in the entire sample were immature. The largest of the immature females in this sample was 8¼ inches total length.

SEX RATIO

The number of specimens, the sex ratio expressed as the percentage of males in the total for the daily collections, and the ratios for the combined collections of each month are shown in table 37 for samples containing 50 or more fish. All samples were obtained from commercial impounding nets. The sex ratio of the individual samples fluctuated rather widely within each month except August, September, and December, 1929, and April 1932. This wide fluctuation points to a segregation of the sexes throughout much of the year. A segregation may occur, however, in a month in which the sex ratio is not highly variable (as the predominance of males in April 1932).

The wide daily variation in the relative abundance of females and males in the samples makes it difficult to determine a truly reliable sex ratio for the perch of Lake Erie. The data in table 37 suggest that a large number of relatively small samples, preferably distributed throughout the season, will permit a more accurate estimate of the relative abundance of the sexes than may be obtained from a few large samples. Table 37 reveals that the average ratio for all samples combined, except those taken in April, was 96 females to 100 males (50.9 percent). The April samples were omitted from the computation because the sex ratio obviously was distorted by the presence of disproportionately large numbers of males.

The April (1928 and 1932) collections were consistent in the strong preponderance of males. The males predominated also in both samples obtained late in May 1929. On the other hand, the females were relatively more abundant in the samples obtained May 9 and 10, 1929. One sample collected during June 1929 indicated that the sexes were segregated, whereas the other showed no marked preponderance of either sex. The data obtained during July 1929 showed an increasing proportion of males as the month advanced. The males were somewhat more abundant than the females in each sample taken during August, but on no date, with the possible exception of August 6, were they strongly predominant. No strong dominance of either sex was evident in the material taken in September. The single October collection contained nearly 70 percent males. Only two of seven samples taken during November (November 26, 1929, and November 7, 1937) showed sufficiently disproportionate representation of the sexes to be interpreted as indicative of segregation. There was little evidence of segregation on the two dates in December. In general, then, it appears that the sexes were segregated during April and May, and probably to some extent during part of June, July, August, October, and November. There is no evidence of any distinct segregation during September and December; however, only two samples were taken in each of these months.

TABLE 37.—*Percentage of males in the daily samples of Lake Erie yellow perch*

Date	Number of specimens	Percentage of males	Date	Number of specimens	Percentage of males
			1929:		
1928: Apr. 30	94	95.7	Nov. 2	72	51.4
1929:			Nov. 12	251	47.0
May 9	110	30.9	Nov. 16	114	57.9
May 10	147	26.5	Nov. 22	51	54.9
May 15	228	74.6	Nov. 26	86	72.1
May 25	132	69.7			
			November, all samples	574	54.2
May, all samples	617	54.3			
			Dec. 4	136	55.1
June 20	563	37.1	Dec. 7	171	57.3
June 29	90	54.4			
			December, all samples	307	56.4
June, all samples	653	39.5			
			1932:		
July 1	202	30.7	Apr. 11	70	75.7
July 6	65	36.9	Apr. 13	63	84.1
July 13	447	48.1			
July 20	114	60.5	April, all samples	133	79.7
July 30	68	64.7			
			1937:		
July, all samples	896	46.2	Nov. 3	65	47.7
			Nov. 7	66	68.2
Aug. 6	252	61.1			
Aug. 17	87	56.3	November, all samples	131	58.0
Aug. 22	86	52.3			
Aug. 26	178	55.6			
Aug. 31	133	52.6			
			Grand total, April excluded	4,313	50.9
August, all samples	736	56.7			
Sept. 3	216	47.2			
Sept. 23	114	55.3			
September, all samples	330	50.0			
Oct. 26	69	69.6			

The reasons for the apparent segregation of the sexes of the Lake Erie yellow perch are largely unknown. The segregation during April and May perhaps was due to the spawning-season habits of the species. A segregation associated with sex differences in feeding habits during the summer months, such as was found by Eschmeyer (1938), may occur. Materials for study of the food of the Lake Erie perch were not available. Another possible factor in the fluctuating sex ratios during the summer is age. The females tend to increase in relative abundance with advancing age; consequently, variation in the age composition of the samples would contribute to an apparent segregation of the sexes. However, this explanation can account for only part of the variation in the sex ratio since the ratios varied widely in samples of fish of the same age but taken on different days of the same month (table 38).

Age determinations of certain of the above materials permit the examination of the relation between the proportional representation of the sexes and age. Table 38 shows the sex ratio of Lake Erie yellow perch in a number of samples, expressed as the percentage of males in the total, by age group. Because of the daily fluctuations in sex ratio the data have been presented for daily catches as well as by the month and for all months combined. In spite of certain exceptions, it may be said that there was a progressive decrease in the proportion of males as the age increased. It is apparent that either the relative abundance of males in the stock was progressively less with each yearly increase in age, or that the females were progressively more available to the fishery.

TABLE 38.—*Percentage of male Lake Erie yellow perch by age groups, according to date of capture*

[Total number of specimens in parentheses]

Date	Age group				
	I	II	III	IV	V
1929:					
July 1	----------	38.5(13)	26.7(131)	12.5(16)	0(1)
Sept. 23	0(1)	33.3(9)	57.7(104)	----------	------
Nov. 12	83.3(18)	49.4(83)	43.8(121)	33.3(27)	0(2)
Nov. 16	80.0(5)	55.8(52)	57.4(54)	66.7(3)	------
Nov. 26	80.0(5)	74.3(35)	67.4(43)	100.0(3)	------
November, all samples	82.1(28)	56.5(170)	51.8(218)	42.4(33)	0(2)
Dec. 4	83.3(6)	52.7(55)	56.1(66)	44.4(9)	------
Dec. 7	69.4(36)	51.8(83)	59.2(49)	66.7(3)	------
December, all samples	71.4(42)	52.2(138)	56.5(115)	50.0(12)	------
1932:					
Apr. 11	----------	100.0(2)	83.3(48)	55.0(20)	------
Apr. 13	----------	----------	88.0(50)	69.2(13)	------
April, all samples	----------	100.0(2)	85.7(98)	60.6(33)	------
1937:					
Nov. 3	71.4(28)	31.4(35)	0(2)	----------	------
Nov. 7	73.5(34)	61.3(31)	100.0(1)	----------	------
November, all samples	72.6(62)	45.5(66)	33.3(3)	----------	------
Grand total, April excluded	73.7(133)	52.0(396)	48.0(571)	36.1(61)	0(3)

Sex differences in the age of entry into the fishery can produce an "apparent" change in the sex ratio with increase in age. The earlier attainment of maturity by the males, together with their apparent tendency to remain on the spawning grounds longer than the females, doubtless accounted for the great preponderance of males in age groups I and II and their abundance in age group III of the spawning-run (April 1932) collection. Consequently, the decrease in relative abundance of males with increase in age in that collection cannot be accepted as descriptive of the general population. Significance must be ascribed, however, to the fact that a similar, if less pronounced, change in the sex ratio occurred in the collections of other months when there is no reason to believe that a segregation on the basis of maturity existed. In a majority of the samples taken in months other than April the males exhibited a tendency to decrease in relative abundance with increase in age. It may be concluded that this tendency of the males is a real and not an apparent characteristic of the Lake Erie yellow perch.

The acceptance of a shifting sex ratio with age as characteristic of the Lake Erie yellow perch population carried with it the assumption of a differential mortality of the sexes. This difference in death rate may have its origin in a selective destruction in the fishery or it may depend on sex differences in the natural mortality rate.

It would appear that a differential destruction of the sexes by the fishery is the most plausible explanation of the changes in sex ratio with age of the Lake Erie yellow perch. The males mature at a younger age, and consequently, are taken by the nets during the spawning season earlier in life than are the females. Furthermore, the apparent tendency for the males to arrive earlier and stay longer than the females on the spawning grounds increases the chances of capture for any particular male, and presumably would

result in effect in a more intensive fishery for that sex. The monthly records of the Ohio Division of Conservation for the years 1930, 1931, 1939, and 1940 [15] reveal that during those years the spawning-season fishery (April and May) produced 28.3 percent of the perch caught during the entire year in Ohio waters. Fishing intensity during the spawning season, when the males predominate in the catches, is therefore sufficiently great to account for an important differential destruction of the sexes. The apparent preponderance of females during early May would reduce, but probably not eliminate, the effect of the spawning-season fishery on the changes in the sex ratio. It seems impossible to escape the conclusion that the changes in sex ratio with age of the Lake Erie yellow perch were caused in large measure by a differential destruction by the fishery chiefly during the spawning season.

It should be mentioned that the minimum legal size operates to reduce the effect of the differential destruction of the males in the spawning-run fishery. Large numbers of mature but illegal-sized males on the grounds are captured but returned to the lake. However, it is known that about 14 percent of the illegal-sized yellow perch are destroyed, or seriously injured, when the nets are lifted. It is not improbable that the total destruction of illegal-sized males during a spawning season is considerable, in spite of the fact that none enters the commercial catch.

Other factors that might have had an influence on the changes in sex ratio with age will be mentioned briefly. Geiser (1923, 1924a, 1924b) concluded that the females (of fishes, as of many other animals) are inherently more viable than the males under adverse conditions. Hile (1936) stated that a differential natural mortality was the most probable cause of the changes in sex ratio of the cisco, *Leucichthys artedi*, with age. There is no fishery for the cisco in the Wisconsin lakes whose populations he studied. Hile pointed out further that there was no basis for any assumption of a differential destruction of the sexes by predatory forms. Any possible effect of a differential natural mortality of the sexes would be obscured in the Lake Erie yellow perch because of the differential destruction by the fishery.

SUMMARY

1. The annual production of yellow perch from the United States waters of Lake Erie fluctuated about an average of 3 million pounds in the early (1885–99) period of the fishery. The average declined to about 2 million pounds in 1900–1927, increased to over 7½ million pounds in 1928–35, and fell to about 2½ million pounds in 1936–47. There was a definite tendency for the variability in annual production to increase in each succeeding period except the most recent one (1936–47). The trend in average annual production from the Ontario waters was similar to that in United States waters only in the last two periods, 1928–35 and 1926–47. The factors of fishing intensity (increases in the number of nets, and improvements in nets, boats, and methods of lifting gear), changes in fishery laws and the administration of the laws, and abundance were considered in evaluating both the long- and short-period trends in the annual production of Lake Erie yellow perch.

2. In this study, age determinations and growth calculations were made from examination and measurement of the scales of 4,377 yellow perch taken by trap nets from Lake Erie. In addition, ages were determined of 576 specimens employed in a special study of the relation between body length and scale length, and of 1,566 fish taken by gill nets. Analysis of the length-weight relation was based on 23,158 specimens, and the length frequencies were compiled from the measurements of 59,779 individuals. The materials were collected during the years 1927 to 1930, and in 1932, 1934, 1937, and 1943 to 1948. Data from the different sections of the lake were combined after preliminary examinations revealed the combination justifiable.

3. Validity of the use of annuli on the scales of the yellow perch as year marks was established for the first time on the basis of the following observations: (a) The 1927, 1928, and 1929 collections were dominated by the same year class that was represented by larger and, according to scale readings, older fish in each succeeding year; (b) the annulus was on the margin of the scale in the early season but was progressively farther from the margin in mid-July, September, and December; (c) the lengths calculated from scale measurements for different years of life agreed

[15] These four years are the only ones close to the period during which sex data were obtained for which monthly records of catch are available.

rather closely with the empirical lengths of fish shown by scale readings to have completed the same number of years of life, and lengths calculated for the same year of life agreed more closely with each other than with lengths computed for any other year regardless of the age of the fish employed in the calculations.

4. The more important criteria employed to determine the presence of an annulus were the discontinuity between successive growth fields which resulted in well-defined "cutting over" of the circuli, particularly in the lateral region of the scale, and the fragmented, irregular appearance of the last circulus laid down in each growing season. False annuli occurred but it is believed they usually could be detected by the lack of cutting over, their generally indefinite appearance, and their position with respect to true annuli. About 5 percent of the scales were discarded as unfit for age determinations.

5. Annulus formation may be completed as late as July 1 in some years. In spite of the apparent coincidence of spawning and the completion of the annulus in some years, the annulus cannot be considered as a spawning mark since immature individuals form annuli identical in appearance with those formed by mature fish, and the characteristics of a typical spawning mark as found on the scales of other fish are absent from yellow perch scales.

6. Detailed data are provided on the relation between body length and scale length of the American yellow perch.

7. The Dahl-Lea method of calculating lengths by direct proportion was applicable to the yellow perch when the calculated standard lengths were 96 mm. (4.5 inches total length) or greater. When these lengths were less than 4.5 inches they were corrected by use of a table containing the corrected length corresponding to each length computed by direct proportion. These corrected calculated lengths, derived from an empirical curve of the body-scale relation, were always greater than the uncorrected lengths. Correction of the computed lengths failed, however, to eliminate the discrepancies between corresponding lengths calculated for different age groups.

8. Discrepancies occurred between corresponding calculated lengths in all years of life. The computed lengths for any one year of life decreased progressively as the fish for which the computations were made became older. Discrepancies in first-year calculated lengths were small among age groups older than group I.

9. The discrepancies in calculated lengths were shown to represent real rather than "apparent" differences in growth since large errors could not result from the method of calculation.

10. It was concluded that the selective action of gear, selection according to maturity at the time of the spawning run, and selection according to legal-size limit, all of which doubtless produced a selective destruction of the more rapidly growing individuals in the fishery, were the chief causes of the discrepancies in the calculated growth of the Lake Erie yellow perch, but that a differential natural mortality, correlated with rate of growth, was a possible supplementary factor. The presence of discrepancies between corresponding calculated lengths of different age groups of the same year class proved that annual fluctuations in growth rate were not an important source of the discrepancies in calculated lengths.

11. The females grew in length a little more rapidly than the males during the first year of life, at the same rate in the second year, and more rapidly in all later years.

12. The annual increments of growth in length decreased progressively with age in both sexes.

13. Growth compensation occurred in the Lake Erie yellow perch, but usually did not appear before the third year of life. The difference in average length between the largest and smallest yearlings was maintained or increased in the second year.

14. It was estimated that the proportions of growth completed at the end of the different months of the 1928 and 1929 seasons were 15 percent for June, 50 percent for July, 80 percent for August, and 100 percent for September. However, growth continued through October in 1927.

15. Significant correlations could not be demonstrated between annual fluctuations in growth rate and precipitation, percentage of possible sunshine, and mean wind velocity. Significant positive correlations were determined, however, between growth and mean air temperatures for the following combinations of months: May, July, and September; May and September; July and September. Mean air temperatures in August exhibited significant negative correlation with annual fluctuations in growth rate.

16. The yellow perch of Lake Erie grew more rapidly than did most of the perch of other waters with which comparisons were made.

17. Scales of Lake Erie yellow perch used by Harkness (1922) were compared with those in the present study, and the annual increments of calculated length indicated no pronounced change in the growth rate of 1927 from that of 1920.

18. Length frequencies of the impounding-net collections had a unimodal distribution each year, but gill-net collections showed both unimodal and bimodal distributions.

19. The position of the mode in the length frequencies fluctuated from year to year, and was influenced to a considerable extent by the average length of the dominant age group. The modal frequency fluctuated over a wider range in the impounding-net collections than in the gilled fish from gill nets because of the greater selectivity of the latter gear.

20. The coefficient of condition K of individual Lake Erie yellow perch ranged from 1.13 to 3.23, and averaged 1.91. The state of the gonads affected the coefficient of condition of the females during the spawning season, at which time they lost approximately 16 percent of their prespawning weight. There are no data on the loss of weight of males at spawning. At other periods condition was not related to sex or state of maturity.

21. The coefficient of condition increased sharply from June to July and remained at a high level in August and September. In two of three years condition declined in the autumn, but in the third year it improved.

22. Weight of the Lake Erie yellow perch increased at a rate slightly greater than the cube of the length. Over the interval of length to which the equation was fitted the empirical and calculated weights agreed closely.

23. The year class of 1926 was unusually strong and dominated the impounding-net catches of 1927, 1928, and 1929. There is evidence from the samples of legal-sized yellow perch that the 1942 year class also was one of exceptional strength. The year classes of 1936 and 1944 are believed to have been of more than ordinary size.

24. No relation between strength of year classes and meteorologic conditions could be demonstrated.

25. The commercial catch (legal size) of both impounding and gill nets was dominated by age group III in the spring and early summer. Dominance by group-II fish was characteristic of the late-season catches of both types of gear, although there are exceptions when age group III may be dominant in both gears during the autumn.

26. The sex ratio was determined to be 96 females to 100 males in the combined data from all samples except those obtained in April, when the ratio was obviously distorted. Evidence was obtained of segregation according to sex in all months from April to November, inclusive, except September. It was pointed out that the number of samples employed, as well as the number of individuals examined, was important in the accurate determination of the sex ratio. The relative abundance of females in a year class increased with age.

27. Male yellow perch in Lake Erie matured at an earlier age and at a smaller size than females. Practically all males were mature or maturing at a total length of 8 inches. Proportions of females mature or maturing at different total lengths were 48.4 percent at 8 to 8½ inches, 86.1 percent at 8½ to 9 inches, and 97 percent at 9 to 9½ inches.

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UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

FLOUNDERS OF THE GENUS *PARALICHTHYS* AND RELATED GENERA IN AMERICAN WATERS

By Isaac Ginsburg

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CONTENTS

	Page
Common names	269
Sampling	269
Structural differences distinguishing the species	269
Scales	270
Gill rakers	272
Anal rays	273
Dorsal rays	274
Correlation in the numbers of anal rays and gill rakers	274
Frequency polygons	276
Color pattern	277
Proportional measurements	280
Change of form with size	281
Specimens at the border line	282
Generic limits	284
Key to the American species	285
Hippoglossina	287
Subgenus Hippoglossina	288
H. bollmani	288
H. mystacium	289
H. stomata	289
H. macrops	291
Subgenus Lioglossina	293
H. oblonga	293
H. tetrophthalmus	297
Pseudorhombus	298
P. isosceles	299
Paralichthys	300
Subgenus Paralichthys	301
P. microps	301
P. patagonicus	301
P. hilgendorfii	304
P. schmitti	305
P. fernandezianus	305
P. adspersus	306
P. californicus	307
P. aestuarius	310
Subgenus Chaenopsetta	312
P. woolmani	312
P. brasiliensis	314
P. dentatus	316
P. albigutta	324
P. vorax	327
P. tropicus	327
P. lethostigma	328
P. squamilentus	332
Species of doubtful relationship	334
Paralichthys triocellatus	334
Paralichthys coeruleosticta	335
Hippoglossus kingii	335

FLOUNDERS OF THE GENUS *PARALICHTHYS* AND RELATED GENERA IN AMERICAN WATERS

By ISAAC GINSBURG, *Fishery Research Biologist*

This report is an account of the important group of flatfishes belonging to the genus *Paralichthys*, and the closely related genera *Hippoglossina* and *Pseudorhombus*, which occur in American waters and, in the aggregate, are food fishes of great economic importance. Three of the leading species, the summer flounder, the southern flounder, and the California halibut, add annually nearly 20 million pounds to the commercial catch of the United States. Statistics are not available for some other species which are of lesser economic importance or occur on the coasts of Central and South America. The combined catch of all the lesser species is probably considerable at present and will very likely increase with future advances in exploitation of the natural resources of the American continents. In view of the importance of these species, it is remarkable how little we know of their biology. Such knowledge is a prerequisite to the wise exploitation of any species. This report presents some basic knowledge of the species, derived from first-hand, accurately determined data, which is necessary to their further study.

In order to understand properly the species of *Paralichthys*, it is necessary to consider also those that belong to *Hippoglossina* and *Pseudorhombus*, as the species of these three genera form an interrelated, closely knit, and compact group. A serious drawback to a rational study of their life histories is the difficulty of properly distinguishing the species, which are so closely related that where two or more occur together considerable difficulty has been encountered in trying to refer specimens to their respective species. It is true that Jordan and Gilbert (Bull. U. S. Nat. Mus., 16: 822–823, 1883) long ago indicated in broad outline the structural characters by which the common species may be distinguished; but in *Paralichthys* that did not prove sufficient. Descriptions based on a few specimens may be of use in separating material in bulk, but they are insufficient to identify a considerable percentage of individual fish. The chief characters distinguishing the species are of a meristic nature. The extent of intraspecific variations in these characters is considerable. Moreover, the species are closely related and they approach one another or even intergrade somewhat in these characters. Consequently, when specimens at or near the border line with respect to one or more structural characters are examined, they appear to be inseparable specifically, and doubt is thus cast on the distinctness of the species.

The difficulties encountered in properly distinguishing the species concerned may be appreciated by a consideration of two treatises dealing with those species. Hildebrand and Cable (Bull. U. S. Bureau of Fisheries 46:464, 1930) state: ". . . the present writers are unable to separate the representatives of this genus [*Paralichthys*], occurring locally [at Beaufort, N. C.], into more than two groups (species?) . . ." The fact is that three common species are present at Beaufort. The data given by these authors on the chief differentiating characters nearly agree with those determined by me. Many of their specimens formed the basis of my studies. Their figures 79–81 representing the frequency distributions of the numbers of gill rakers and anal and dorsal rays evidently are bimodal polygons which, taken separately, would understandably lead to the statement quoted above. However, it is of the utmost importance to correlate the data on which the polygons are based. To illustrate, their figure 79 consists of two well-defined polygons which touch at a point, and seemingly it represents not more than two species. However, were the frequency distributions of the number of anal rays of the specimens represented in the left polygon graphed separately, the result would be a polygon similar to their figure 80. That is, the left polygon represents two species, *albigutta* and *lethostigma*, while the right polygon represents *dentatus*. Similarly we may use their figure 80

as the starting point of the correlation. It consists of two somewhat irregular polygons which, considered independently, might also be taken to represent two species. Were the number of gill rakers of the specimens represented by the right polygon graphed separately, the result would be a bimodal polygon similar to their figure 79, which would represent two species, *lethostigma* and *dentatus;* while the left polygon of figure 80 represents *albigutta.* A comparison of Hildebrand and Cable's figures 79–81 with figures 1–3 of this report will clarify the preceding discussion. The intraspecific variability and distribution of the three characters concerned, among the three common species, are such that when a mixture of specimens of the three species is studied and the mixed data graphed for each character separately, as was done by Hildebrand and Cable, the resulting polygons would be similar to their figures 79–81, leading to the conclusion that not more than two species are involved. But when the characters are correlated it becomes clear that three distinct and common species are represented. Moreover, after correlating the characters and dividing the mass of specimens into three rather well-defined species, other characters appear which although not sufficiently divergent to separate all the specimens will yet distinguish the great bulk of specimens of the three species, respectively.

Norman [1] states: "[*albigutta* is] perhaps identical with *P. lethostigma* . . ." (p. 75); and ". . . it is possible that *lethostigma*, *albigutta* and *squamilentus* will eventually have to be regarded as representing one variable species" (p. 76). However, when adequate samples of the three species about which Norman was in doubt are studied and the data correlated and tabulated, as is done in the following pages, all questions as to their distinctness disappear. While Norman tentatively did treat these three species as distinct, he did not properly separate all his western Atlantic specimens.[2]

In order to prove that the separate species are distinct, and to show how individual fish may be identified, it becomes necessary to investigate the chief distinguishing characters by statistical methods; in other words, it is necessary to determine in detail the variability of these characters of each species separately, showing precisely their limits and their normal frequency distributions, and to correlate them. That has been accomplished during the present study for the common species, as far as available material permits. It now becomes a comparatively easy matter to separate the species. There is seldom trouble in placing individual specimens, certainly not more so than in many other closely related species.

A study such as that reported in the following pages manifestly must precede any consistent study of the life history of each species. Besides studying their taxonomy, the known and scattered data regarding the biology and the economics of the species have been digested and condensed, and original observations included. This paper treats of those species that inhabit the Atlantic and Pacific coasts of North and South America. The species are so closely interrelated that it is necessary to treat them as a group in order to understand them fully.

In stating proportional measurements of certain parts throughout this paper, the figures given refer to percentage of the standard length. Statements of the size of specimens refer to the total length, including the caudal fin. Measurements of the eyeball and orbit are those of the upper eye. The stated number of scales refers to the number of rows over the straight part of the lateral line unless otherwise specified (p. 271). The diagnoses include only those characters which are of importance in distinguishing the species. Counts and relative proportions are mostly given in general statements in the diagnoses. More detailed data are in the tables which form part of and should be used in connection with the diagnoses.

In the following accounts of the species, the given numbers of specimens examined are those in the United States National Museum Catalog, unless otherwise indicated.

All illustrations accompanying this paper, executed with such obvious skill, were prepared by Louella E. Cable. Figures of specimens represent reworked photographs, which were made in the Smithsonian photographic laboratory.

[1] A systematic monograph of the Flatfishes (Heterosomata) vol. 1, Psettodidae, Bothidae, Pleuronectidae, by J. R. Norman, British Museum, London, 1934.

[2] See Ginsburg, Jour. Washington Acad. Sci., vol. 26, pp. 130–133, 1936. In that paper I discuss briefly some of the differences between the present treatment of the species and that in Norman's work. Where necessary the discussions are here amplified under the accounts of some of the species.

COMMON NAMES

Since these flounders are common or abundant food fishes, it is especially desirable for each species to have a distinctive common name which may be uniformly applied to the same species throughout its range. An attempt is here made to introduce such common names for the species of *Paralichthys* that occur in the waters of the United States. It is well known to those who deal with the fishes of the country as a whole that the multitude of common names applied to a given species is confusing, especially with food fishes that enter the channels of trade. Not only are species often known by different names in different sections of the country, but frequently this occurs in adjacent communities of the same State. It is even more confusing when a name is applied in one locality to a particular species, and in another to an entirely different species. In this paper, therefore, a distinctive English name is suggested as a uniform common name for the species.

SAMPLING

The chief characters used for separating the species are of a meristic nature and vary within rather wide limits. The variations are of the usual frequency-distribution type and lend themselves readily to the ordinary methods of statistical studies of such variations. It is evident, therefore, that in any study of these characters it is important to sample the individuals examined in such a manner that the resulting frequency distribution, as tabulated, represents as nearly as possible the living population of the species in the water.

The importance of a representative sample in studies of fin ray counts for instance, is forcibly impressed after gaining considerable experience in such studies. It may be readily observed in species in which the number of fin rays varies within considerable limits that specimens obtained in the same haul of the net will sometimes tend to group themselves either near the beginning or near the end of the frequency distribution of the species as a whole. Therefore, in order to portray adequately the meristic characters for each species, the method of selecting the sample to be studied is of importance. If, let us say, the fin rays of one hundred specimens are enumerated and tabulated, and all the specimens are obtained in a single haul of the net, the result is apt not to present a true picture of the species. On the other hand, if the hundred specimens are taken at random, one each, from as many hauls in different localities, the result is apt to present a fairly good view of the normal variation of that character within the species as a whole. The individuals employed in this study represent specimens obtained by methods intermediate between these two extremes. They were those obtained in the ordinary course of extensive collecting, when the tendency on the part of the collector is to save a few specimens out of each haul as a sample, especially when any haul yields too many individuals of one species. All the individuals tabulated herewith are a composite of many such samples generally ranging from 1 to 10 specimens in each sample. Only three samples had more than 10 specimens, the highest number being 21. The frequency distributions thus obtained for the more common species probably represent fairly those of the respective species, at least near enough for practical purposes. (The question is further discussed on p. 276 in relation to the three common east-coast species.)

STRUCTURAL DIFFERENCES DISTINGUISHING THE SPECIES

For the practical purpose of the proper distinction of the three common eastern species, it is only necessary to enumerate correctly for any given specimen, the gill rakers, the anal rays, the dorsal rays, and the scales. The importance of the characters is in the order stated. These structural characters in combination with evident differences in the color pattern will serve to distinguish individual fish of the three common species of the east coast. Proportional measurements in the east coast species are generally of secondary importance. However, when all the species are taken into consideration these generalizations do not hold altogether, and the important differentiating characters are pointed out under each species. Also, when all the species of the genus are considered, the structure of the scales, whether cycloid or ctenoid, and the presence or absence of accessory scales is of much importance in classification.

In distinguishing the species in general, reliance must be placed to a large extent on the number of

gill rakers, fin rays, and scales. As these numbers vary within wide limits within the species, and individual fish of closely related species may approach or even overlap in these respects, it is evident that the course of the student in his attempt to properly distinguish the species is beset with many pitfalls. By way of illustration, it may be pointed out that a specimen of *lethostigma*, for instance, having 65 rays in the anal fin may be considered as conspecific with a specimen of *albigutta* having 62 rays, rather than with another specimen of *lethostigma* having 72 rays, as far as this one character is concerned. Of course, in the proper identification of any given specimen all the characters must be taken into account, but the student will be greatly aided in reaching the correct conclusion, if instead of the simple range of each meristic character, he has before him tables showing the frequency distributions of these characters. Such tables are therefore supplied here, as far as available material permitted. In addition to their practical value, the tables afford valuable evidence going to prove the distinctness of closely related species, where doubt may exist.

TABLE 1.—*Frequency distribution by number of oblique rows of scales over straight part of lateral line to end of hypural.*

Species	Number of scales																																		
	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
Hippoglossina																																					
bollmani	1		1	2	2																																
mystacium								1																													
stomata	1		2	1	1		3	1	1	2		1																									
oblonga																			1		1		2	2	2	1	4	3	1	2	1	1	2	1		2	1
tetrophthalmus																			2						1												
Pseudorhombus																																					
isosceles		2				1																															
Paralichthys																																					
patagonicus																								1								1					
schmitti																																					
adspersus																			1		1	1			1	1	2	2	1	1	1	1	1	1	1		1
californicus																		2	3	2	4	4	7	5	3	6	2	4	5	1		1	1	1			
aestuarius																				2	2	4	6	5	1	2		3		1	2	2	1		1		
woolmani																		2	1	2	1	1	3	1	2	2	1										
brasiliensis																		1	2	1	3	2	3	1	2	1		1									
dentatus												1	2		1	2	2	8	11	8	16	11	5	7	8	7	4	3	1	3	2	1					
albigutta			2	1	5	5	7	18	16	10	9	8	6			2																				
vorax				1																																	
tropicus																							1														
lethostigma								1	1	1	3	12	11	15	17	20	8	7	11	8	5	5	5		1					1							
squamilentus																							1		1	1	1	2			2	1		2		1	

SCALES

The cycloid or ctenoid character of the scales is of primary importance in the major division of the species comprising the genus *Paralichthys* and is of much help in the identification of the species of this genus as well as of related genera. In the Fishes of North and Middle America, by Jordan and Evermann (Bull. U. S. Nat. Mus., No. 47, Pt. 3, 1898), a general work used by ichthyologists to identify American fishes, this character is inadequately treated. In the definition of the genus (ibid. p. 2624) the statement is made "scales small, weakly ctenoid or ciliated." This is not true of all the species; and in the descriptions of some of the species the scales are correctly described as "smooth" or "cycloid." It is interesting to note that in the same work, the two genera which are closely related to *Paralichthys*, namely, *Hippoglossina* (p. 2620) and *Lioglossina* (p. 2622), as limited by those authors, are distinguished by the scales, ctenoid in one and cycloid in the other. This character is also of importance in forming major divisions of the species comprising the genus *Paralichthys*. The presence or absence of spinules on the scales was found to be the most constant of all characters used in the distinction of the species, with the exception of *P. aestuarius* and *Hippoglossina oblonga* (the latter species being assigned to *Paralichthys* by Jordan and Evermann in the work cited). In *H. oblonga* the number of spinuliferous scales is highly variable, but a few are always present on the caudal peduncle of the blind side in specimens over 75 mm. long, and the eyed side of the head always has spinuliferous scales in large specimens. In *P. aestuarius*, it is an age character, the scales of the eyed side being all spinuliferous in fish less than about 160 mm. in length. The spinules are gradually lost after that length has been reached; the scales become cycloid in specimens over 220 mm. In the other

species, this character is constant at all ages, although in very large fish the spinules in the species having them sometimes are comparatively less marked. In very large specimens they sometimes change to coarsely granular asperities, but the distinguishing nature of the scales is still evident. The two exceptional species in this respect, and the change of the scales in very large specimens of other species perhaps explains the inadequate treatment this character has received in the study of the species of *Paralichthys*. However, the structure of the scales is of as much importance in interpreting the relationship of the species and in the practice of identification, as it is in related genera. Besides the presence or absence of spinules on the scales, another important character which may be used in generic division is the presence or absence of accessory scales (see p. 284).

Besides the structure of the scales, their size, which is usually expressed inversely as the number along certain lines of the body, is a valuable aid in distinguishing the species when used in connection with the other characters, although it usually shows much variability and considerable intergradation. One serious drawback to a precise use of this character is the difficulty of determining the number of scales with any reasonable degree of accuracy. The tubes in the lateral line are easiest to count in young fish, but the more or less clear-cut boundaries between the individual tubes disappear to a large extent with growth. Also, with increase in size the normal scales on either side gradually overlap more and more those in the lateral line, while the increasing numbers of accessory scales cover the surface of all the large scales more and more. Consequently, in large or medium-sized fish, it is almost impossible to count the individual scales in the lateral line with any reasonable degree of accuracy.

After testing different methods of expressing the scale count, the following procedure was adopted as yielding fairly accurate results with the least amount of labor. The count is made of the number of oblique rows over the straight part of the lateral line, beginning with the row standing directly over that canal in the lateral line which is entirely, or almost entirely, horizontal and ending with the row the lowest scale of which is at the end of the hypural as determined by flexing the caudal fin. In counting the scales the specimen is held with the back tilted down and away from the observer. When held in this position the reflection of light is such that the rows of scales appear fairly prominent, and the rows are counted rather than the individual scales. Sometimes the fish has to be turned somewhat at different angles until the rows become prominently visible so that they may be counted with any fair degree of accuracy. A check on a number of small specimens shows that the number of scales in the lateral line closely approximates the number of oblique rows placed over it.

The number of rows along the curved part of the lateral line cannot be determined with as much accuracy as along the straight part, because the rows in the anterior part of the body are more irregular, and because of the greater difficulty of fixing the point to begin the count. Had these rows been included in the count, the small increase in the degree of specific divergence would have been made at the sacrifice of greater accuracy. They were, therefore, omitted and the number of scales stated in the diagnoses in this paper and in table 1 uniformly refers to the number of oblique rows over the straight part of the lateral line

In current descriptions, the number of scales is usually stated as so many or "about" so many in the lateral line. It seems desirable to have some conversion factor by which current descriptions may be correlated with the present paper, although it seems highly probable that counts hitherto recorded by different investigators are not comparable by a wide margin, because of the use of different methods. The number of scales in the curve was determined on a number of small specimens in which they may be counted with a fair degree of accuracy. It was found that, in general, that number closely approximates one-half of the number in the straight part. Therefore, by adding one-half to the number given in this paper, counts of scales are obtained which are approximately comparable with those given in current descriptions. In the short accounts of established species of which no specimens were examined the number of scales stated is that obtained by using the above conversion factor and subtracting the estimated numbers in the arch from the number in the entire lateral line.

GILL RAKERS

Next to the structure of the scales the number of gill rakers constitutes the most valuable character for separating the American species. It has been universally so used and its importance justly emphasized. For the three common species of the east coast, figure 1 shows unquestionably that *dentatus* is distinct from the other two. Frequency distributions of all the species studied are shown in tables 2 to 4. The number of gill rakers as recorded may vary somewhat with the observer. For instance, in *dentatus* the uppermost gill raker on the upper limb is sometimes very small. Less frequently, this is also true of the anteriormost gill raker of the lower limb. In this investigation the smallest gill rakers were included if they were large enough to be manipulated with a dissecting needle. In *albigutta* and *lethostigma*, slight discrepancies in the counts made by different investigators would be due chiefly to the variability in the uppermost gill raker of the upper limb. This gill raker is sometimes very small, later becoming closely adherent to the gill arch as a triangular piece of cartilage, and finally, seeming to merge with the gill arch. Frequently, when grown to the

TABLE 2.—*Frequency distribution by number of gill rakers on the upper limb of the first gill arch*

Species	Number of gill rakers on upper limb										
	1	2	3	4	5	6	7	8	9	10	11
Hippoglossina bollmani		3	3								
mystacium					1						
stomata				6	8	1					
oblonga [1]	3	23	1								
tetrophthalmus		4									
Pseudorhombus isosceles [1]	3										
Paralichthys											
patagonicus		1									
schmitti			1								
adspersus							12	5			
californicus							14	53	30	4	1
aestuarius						1	11	21	4		
woolmani				9	12	1					
brasiliensis			1	8	8						
dentatus			2	5	64	41	6				
albigutta		31	63	1							
vorax				1							
tropicus		1									
lethostigma		138	8								
squamilentus			7	6	2						

[1] The short stumps of gill rakers, 3 to 5 in number, on upper limb, not included in the count. Traces of 1 or more gill rakers in other species also not included (see text).

TABLE 3.—*Frequency distribution by number of gill rakers on the lower limb of the first gill arch*

Species	Number of gill rakers on lower limb																
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Hippoglossina bollmani			3	3													
mystacium						1											
stomata					1		6	4	4								
oblonga	1	11	13	2													
tetrophthalmus			1	3													
Pseudorhombus isosceles		1	2														
Paralichthys patagonicus				1													
schmitti			1														
adspersus									1	2	4	7	3				
californicus												5	10	36	29	17	5
aestuarius												6	11	9	10		1
woolmani [1]						2	11	7	2								
brasiliensis								4	8	3	2						
dentatus							4	3	18	44	35	11					
albigutta			9	39	41	4											
vorax						1											
tropicus					1												
lethostigma		7	67	66	6												
squamilentus				5	5	5											

[1] The type specimen has 11 gill rakers on lower limb on eyed side and 13 on blind side, the latter number being included in the table, all the counts having been made on the blind side.

TABLE 4.—*Frequency distribution by number of gill rakers on the outer gill arch*

Species	Total number of gill rakers on outer arch																							
	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Hippoglossina bollmani			2	2	2																			
mystacium									1															
stomata							1		2	6	3	2	1											
oblonga	3	10	12	1	1																			
tetrophthalmus			1	3																				
Pseudorhombus isosceles	1	2																						
Paralichthys patagonicus				1																				
schmitti				1																				
adspersus														1	2	2	7	4	1					
californicus																	2	6	10	26	27	13	12	6
aestuarius																1	1	4	12	14	3	1	1	
woolmani								1	7	6	6	2												
brasiliensis										5	3	4	4	1										
dentatus								2	2	2	2	12	35	23	29	8								
albigutta			4	23	29	32	5																	
vorax								1																
tropicus					1																			
lethostigma		6	63	66	10																			
squamilentus					1	6	5	3																

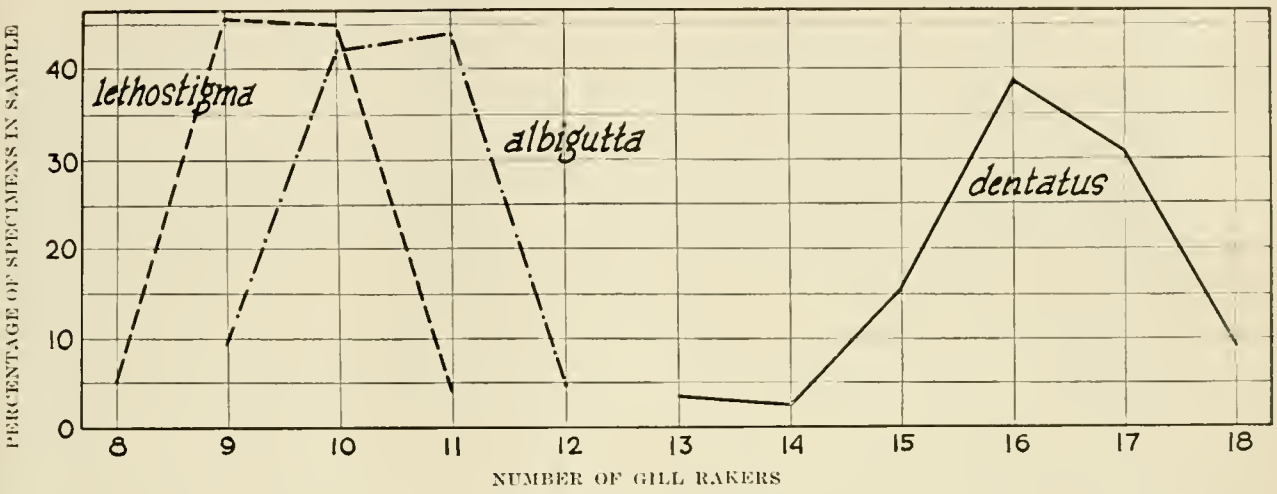

FIGURE 1.—Frequency distribution by number of gill rakers on lower limb of outer gill arch of three common east-coast species of *Paralichthys*. Number of specimens: 115 *dentatus*, 146 *lethostigma*, 93 *albigutta*.

gill arch its triangular outline may be readily traced, but often it is very faint. In this study the uppermost gill raker was arbitrarily included when it projected sufficiently above the surface of the gill arch so that it could be manipulated with a dissecting needle. When it was adherent to the arch even though its outline was evident it was not included in the count. It may also be stated that such specimens are comparatively few, and any slight differences in counts which may be made by different observers would have little effect on the final result when large numbers are studied. In this study all the counts were made by me. The counts of gill rakers as here recorded were all made on the blind side because of greater convenience in counting. The two sides sometimes vary slightly in number; but in the small number of specimens in which counts were made on both sides, as a test, there was no average difference in comparing both sides. The counts were then all made on the blind side for convenience and to insure uniformity.

ANAL RAYS

Next to the gill rakers the number of anal rays constitutes the most important character for separating the three common east coast species, the intergrading individuals being few. This character is especially valuable in separating *albigutta* from both *dentatus* and *lethostigma*. A glance at

TABLE 5.—*Frequency distribution by number of rays in the anal fin*

Species	Number of anal rays																														
	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
Hippoglossina																																
bollmani	1	1	1	2		1																										
mystacium										1																						
stomata		1			1	2	7	1	2	1																						
oblonga													1		1	2	6	1	4	4	1	2		2			1					
tetrophthalmus													1			1	1	1														
Pseudorhombus																																
isosceles																					1	1	1									
Paralichthys																																
patagonicus																					1											
schmitti																		1														
adspersus									1		3	5	6	2	2	1																
californicus				1	4	6	14	26	23	17	16	4	2	2																		
aestuarius												3	2		3	8	5	4	8	3	1	1										
woolmani										4	1	5	5	4	3																	
brasiliensis									2	2	2	5	3	1	1																	
dentatus																1	1		5	4	13	25	21	12	18	6	6	5				
albigutta								1	1	4	10	15	16	26	17	11	5	5														
vorax									1																							
tropicus													1																			
lethostigma																		2	5	10	15	25	27	31	13	14	9	1				1
squamilentus														1	3	3	6	1	2													

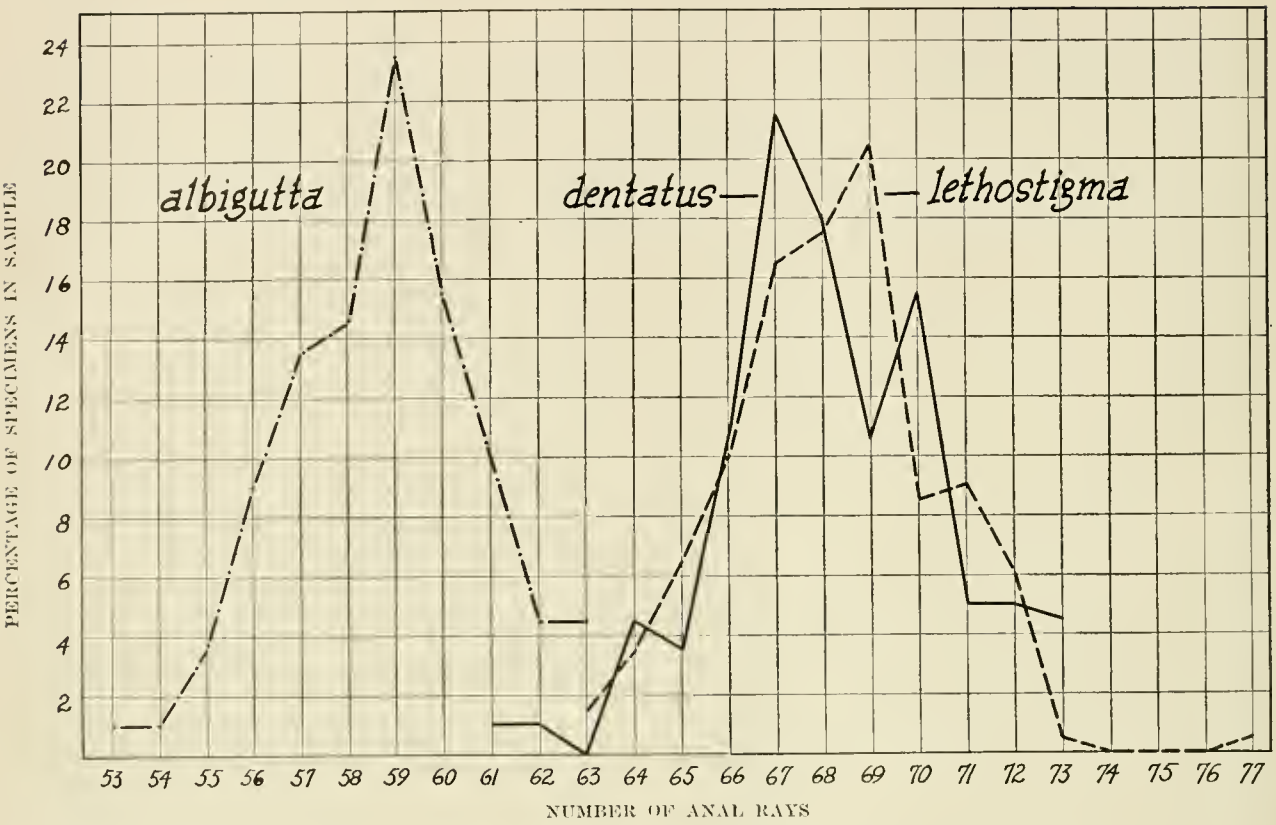

FIGURE 2.—Frequency distribution by number of anal rays of three common east-coast species of *Paralichthys*. Number of specimens: 117 *dentatus*, 153 *lethostigma*, 111 *albigutta*.

figure 2 shows the essential specific divergence of *albigutta* from those two closely related species.

Because the fin ray counts overlap more or less, while at the same time being of prime importance in separating the species, it is essential to make an accurate count when using this character. In this study every fin was counted twice, once on either side, as a check. Since the fin rays are many and the labor of counting tedious, great care and patience must be exercised to insure an accurate count. In practice, some means may suggest themselves to check the counts on both sides of part of the fin. For instance, most specimens have places where the interradial membrane is conspicuously broken. The number of rays up to such a point is jotted down and when the count is made on the other side this number is checked. Again the count may be made in groups of five or ten rays, a dissecting needle being used to point off the groups. By adopting some such means of facilitating the count accuracy is possible.

DORSAL RAYS

Although in the three common eastern species the number of dorsal rays intergrades to a considerable extent (fig. 3), it is a useful character, supplementing the two previous ones for distinguishing doubtful specimens. In the separation of *californicus* from *aestuarius*, the number of dorsal rays intergrades somewhat less than the number of anal rays. The methods of counting and recording the number of dorsal rays were the same as stated for the anal rays.

CORRELATION IN THE NUMBERS OF ANAL RAYS AND GILL RAKERS

Figures 1 to 3 show that the number of gill rakers and that of the anal rays constitute the two most divergent characters. By plotting these two counts, one against the other, in a correlation table (fig. 4), a striking proof of the essential specific divergence of the three common eastern species is obtained. Figure 4 has been prepared from the

TABLE 6.—*Frequency distribution by number of rays in the dorsal fin*

Species	Number of dorsal rays																																				
	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
Hippoglossina																																					
bollmani	1		2	2		1																															
mystacium							1																														
stomata				1	1		3	3	3	3	1																										
oblonga													1	1		1	2	2	2	5	5	3		1		1	2										
tetrophthalmus																	1						1	1		1											
Pseudorhombus																																					
isosceles																							2		1												
Paralichthys																																					
patagonicus																							1														
schmitti																					1																
adspersus									1	3	2	1	3	3	5	1	1																				
californicus							4	7	13	18	15	18	20	7	6	2	1																				
aestuarius																1	3		6	3	5	4	6	5	2	2											
woolmani											2	1	2	3	5	2	2	1	2	1		1															
brasiliensis									1		1		1	2	2	1	3	4	1																		
dentatus																					1	1	1	4	3	9	8	13	21	21	15	5	5	4	3	1	1
albigutta												1	2	4	6	12	10	14	13	15	9	13	6		3	1											
vorax																1																					
tropicus																1																					
lethostigma																					1	4	2	6	15	11	20	18	22	14	11	5	13	2	1	1	
squamilentus																	2	1	1	5	3	2	1	1													

FIGURE 3.—Frequency distribution by number of dorsal rays of three common east-coast species of *Paralichthys*. Number of specimens: 116 *dentatus*, 146 *lethostigma*, 109 *albigutta*.

rough data before attempting to segregate the specimens into their respective species. A mere inspection of figure 4 shows convincingly how the specimens are massed into three fairly well defined groups. These three groups represent: (1) *albigutta* showing a correlation of low gill raker and fin ray counts; (2) *lethostigma* having a combination of relatively few gill rakers and many fin rays; (3) *dentatus* being characterized by relatively many gill rakers in correlation with many fin rays.

While the bulk of the specimens are concentrated at three well separated regions, smaller numbers of specimens radiate diffusely from the three centers of concentration and it is not possible to draw sharp lines of demarcation separating the three species by these characters alone. The proper placement of specimens at or near the border line is discussed on page 282. After such somewhat doubtful specimens are properly placed the boundaries may be drawn between the species with assurance, and they are indicated by a broken

line in the chart. In only one of the squares does the broken line cross. That is, of the total number studied only two specimens of *albigutta* and one of *lethostigma* have the same correlation of the number of gill rakers and anal rays. Such specimens must be assigned to their proper species by means of other characters.

In figure 4 is plotted the total number of gill rakers. Practically the same result is obtained by plotting the number on the lower limb only, except that in that case the lines are more densely grouped.

FREQUENCY POLYGONS

Three variable characters which are of importance in distinguishing the three common species from the east coast of the United States are represented graphically in figures 1 to 3. The polygons representing the number of dorsal rays are markedly irregular; those representing the gill rakers are fairly regular; those representing the anal rays are intermediate with respect to regularity of arrangement. The irregularities are apparently caused by imperfect sampling and may result from one or all of the following main factors. (1) The number of specimens studied may not be sufficient to form a representative sample in its respective species. (2) The method of sampling may be inadequate. (3) The samples do not represent altogether homogeneous populations. It will be shown hereafter (p. 320) that the populations of *dentatus* from Chesapeake Bay and from North Carolina differ appreciably in these three characters. To some extent this is also true of different populations of *lethostigma* (p. 332), and probably also of *albigutta*, although in the latter two species population differences are apparently not so marked. The irregularities in *dentatus* partly disappear when the data are tabulated separately for Chesapeake Bay and North Carolina.

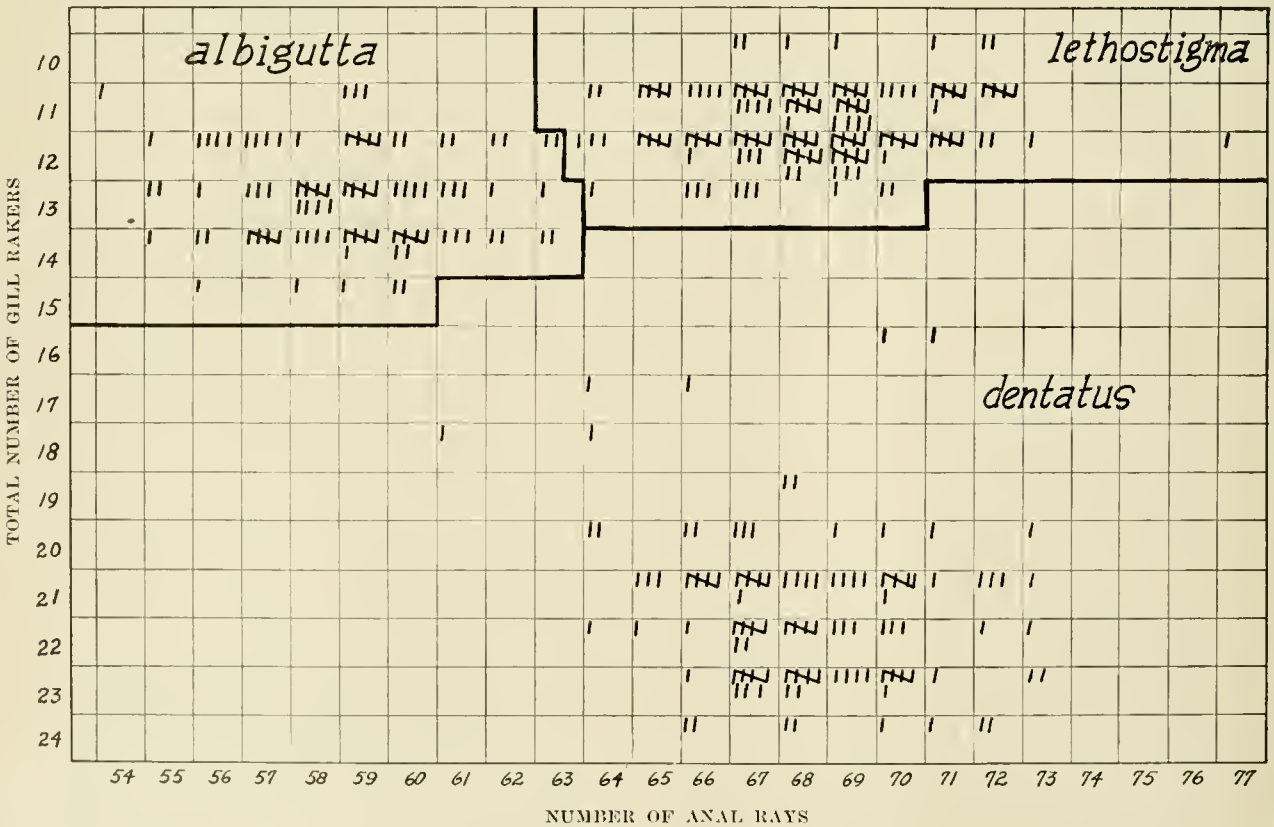

FIGURE 4.—Correlation between total number of gill rakers on first gill arch and number of anal rays, of three common east-coast species of *Paralichthys*. (See p. 274). Each mark represents one specimen; four marks with a cross line represent five specimens.

On the other hand, the marked regularity shown by the distribution of the gill-raker count of *lethostigma* is apparently due to the fact that it is based on material that is not entirely homogeneous. A combination of the somewhat heterogeneous data happened to result in a markedly regular distribution in this case. The more detailed analysis of the data for this count is given on page 332, which shows that the distribution for the combined populations of Texas and Louisiana is not quite so regular as that shown in figure 1. The same may also be true of *albigutta*.

The geographic origin of the specimens forming the basis of the graphs is as follows. The total number of specimens tabulated are *albigutta*, 111; *dentatus*, 120; and *lethostigma*, 159. The three characters were determined for nearly all these specimens; in a few exceptions one or another character was indeterminable on account of injury. The localities of capture of these specimens are: *albigutta*, 71 in a mixed lot from Beaufort, N. C. and Key West, Fla. (see footnote on p. 279), 26 from Texas, 13 from Florida, and 1 from South Carolina; *dentatus*, 71 from Chesapeake Bay, 45 from Beaufort, N. C., 2 from South Carolina, and 2 from Georgia; *lethostigma*, 100 from Louisiana, 34 from Texas, 15 from Beaufort, N. C., 4 from Georgia, and 2 each from Florida, South Carolina, and North Carolina. The great bulk of the specimens in every case thus came from two localities.

Figures 1, 2, and 3 show that we are dealing here with three entirely distinct species, although the samples studied apparently are not altogether representative, and somewhat insufficient as to number. The distributions based on the specimens examined are somewhat irregular and each species differs to some extent with the locality; but the data presented prove conclusively that each species has its own characteristic distribution and fairly well-defined limits. It is evident that a fairly good idea of the specific distributions and their limits may be gained from the determined data; but a study of more specimens and samples more nearly approaching perfection should serve in smoothing the distributions. It is of particular interest to determine further the differences with local stocks in the distributions of the variable characters.

COLOR PATTERN

A cursory examination of the species of *Paralichthys*, in general, shows them to be irregularly blotched. After handling these fishes for some time, however, one may see a definite generalized color pattern; differences in this pattern, on closer examination, are of some aid in distinguishing the species.

The generalized color pattern of the genus may best be discerned in some young fish, especially in those in which the pigment is of medium intensity, neither too dark nor too light. The fundamental, typical color pattern may be said to consist of five longitudinal rows of spots on a variably shaded background, one row along the midline, one under the base of the dorsal, one over the base of the anal and two intermediate rows, one between the median and upper rows and the other between the median and lower rows. (The spots are sometimes rather irregularly arranged and appear to be in 7 irregular rows, see pp. 306, 307, and 312.) The rows may be designated for convenience in discussion as subdorsal, upper intermediate, median, lower intermediate and supra-anal. The spots in the subdorsal and supra-anal rows are generally smaller than in the other three rows. The spots in the median row are generally diffuse, except one spot situated about three-quarters of the way from the gill opening to the base of the caudal fin. In many species this is the most conspicuous spot on the body and in the following discussions it will be designated as the prepeduncular spot.

The value of the color pattern in distinguishing species lies chiefly in the fact that certain spots in certain locations, depending on the species, are most prominent. For instance, in *dentatus*, usually, the three most prominent spots are ocellated and are situated at the angles of an imaginary triangle, the apex of which is formed by the prepeduncular spot, while the base is caudad of the apex and is formed by the two posterior spots of the subdorsal and supra-anal rows, respectively. This will be designated hereafter as the small triangle.

In *albigutta*, the three most prominent spots are also ocellated and form an imaginary triangle, the apex of which is also the prepeduncular spot, as in *dentatus*; the base, however, is situated cephalad of the apex and is formed by the two anterior spots of the upper and lower intermediate rows, respectively. This will be designated as the large triangle. Both of these imaginary triangles are present to a greater or lesser extent in both species.

In *albigutta*, the spots forming the large triangle are the most prominent and nearly always present; those forming the small triangle are less prominent, or faint, or absent altogether. In *dentatus*, the spots in the small triangle are usually the most prominent and nearly always present; those in the large triangle are usually well marked, but not so prominent as the others, often about as prominent, sometimes rather faint. In *lethostigma* all spots are usually rather faint; sometimes the spots in the large triangle are somewhat more prominent, but they are not ocellated. The difference in coloration in the three common species is thus not absolute, it consists of an unequal development in intensity of pigmentation of different parts of the same color pattern. This being the case, and considering also the variability of intensity of pigmentation with individual fish, it may readily be expected that specimens will frequently be encountered which could not be placed by color alone. However, the majority of specimens may be referred to their proper species by color differences. As an illustration, the following test may be cited. A mixed lot of fish consisting of *dentatus*, *albigutta*, and *lethostigma*, from Beaufort, N. C., were separated by color. After the structural differences were studied, it was found that out of a total of 125 individuals thus separated only 14 specimens had been referred to the wrong species: 11 *dentatus* were placed in *albigutta*, two of the latter were tentatively identified with the former, and one *lethostigma* was mistaken for an *albigutta*. It should be stated that this test was made before I had much experience in discerning the color differences of the various species. It may thus be seen that in practice, color is a valuable aid in the proper identification of the species when used in conjunction with the morphological differences, although it is not altogether reliable by itself.

The typical color of the other species could not be well determined with the available specimens, but notes on the color of these specimens are given under the separate accounts of the species.

The spots in the five rows, in general, appear to grow fainter with increased size. To a lesser extent this is also true of the most prominent spots, and in very large specimens the typical specific color pattern is often not discernible.

A similar generalized color pattern is probably present also in *Pseudorhombus* and possibly also in *Hippoglossina* and other related genera, but the material examined is insufficient to determine this definitely for those two genera. In *Hippoglossina* the most prominent spots are in two rows, two or three spots in a row depending on the subgenus, and appear to be situated in the subdorsal and supra-anal rows. In *Pseudorhombus* the location of the most prominent spots differs with the species.

TABLE 7.—*Proportional measurements of 3 species of* Hippoglossina

[Expressed as percentages of standard length]

Species and total length of specimens	Number of specimens	Depth		Maxillary length		Maxillary width		Head [1]		Orbit		Eyeball	
		Range	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range	Average
H. bollmani:													
140–167 mm	6	34.8–38.3	36.4	13.7–14.9	14.3	3.2–3.7	3.5	30.8–32.8	31.9	11.3–12.1	11.8	8.9–9.6	9.2
H. mystacium:													
183 mm	1		39.8		13.6		3.0		30.7		10.4		8.5
H. stomata:													
54–55 mm	2	39.3–40.9	40.1	14.8–15.3	15.1	3.3–3.6	3.5	30.7–32.6	31.7	12.3–14	13.2	10.5–10.5	10.5
116–125 mm	2	38.8–39.6	39.2	14.4–14.9	14.7	3.2–3.4	3.3	31.4–32.7	32.1	11.7–11.8	11.8	8.9–9.7	9.3
138–208 mm	7	36.8–40.7	39.2	14.6–16.1	15.4	3.6–4.2	3.8	31.5–33.7	32.3	10.9–11.7	11.3	7.8–8.9	8.4
240–332 mm	4	38.4–42.4	40.2	16.5–17.9	16.9	4.0–4.6	4.2	33.4–35.6	34.3	10.9–11.6	11.3	7.3–7.6	7.5

[1] Measurements not including the soft scaleless border.

TABLE 8.—*Proportional measurements of some species of* Paralichthys

[Expressed as percentages of standard length]

Species and total length of specimens	Number of specimens	Depth		Maxillary		Head [1]		Interorbital [2]	
		Range	Average	Range	Average	Range	Average	Range	Average
P. adspersus:									
37–45 mm	3	44.6–45.6	45.0	13.2–13.5	13.4	32.9–34.9	34.0		
74–86 mm	3	46.1–47.2	46.7	13.2–14.1	13.7	30.2–32.0	31.3	2.4–2.6	2.5
90–118 mm	6	44.5–48.0	46.7	12.9–13.9	13.5	29.1–31.3	30.1	2.1–2.6	2.4
205 mm	1		45.5		14.1		29.8		3.5
222–276 mm	5	44.2–47.1	45.9	13.3–14.5	13.8	28.4–30.2	29.4	2.9–3.4	3.2
388 mm	1		47.6		13.5		28.9		4.1
P. californicus:									
42–52 mm	3	40.2–41.5	40.7	13.3–15.0	14.3	30.8–33.8	32.7		
61–85 mm	23	37.2–42.3	40.2	13.3–15.2	14.3	27.9–31.9	30.3	1.6–2.5	2.0
94–120 mm	13	37.7–43.5	39.7	12.9–14.3	13.8	27.7–29.4	28.7	1.7–2.6	2.1
124–209 mm	41	37.2–41.7	39.5	12.6–14.9	13.7	26.4–29.8	28.1	1.9–3.0	2.5
226–302 mm	11	37.3–42.4	39.5	12.7–14.0	13.4	26.1–28.0	27.2	2.8–3.3	3.0
332–371 mm	3	38.0–40.8	39.2	12.6–13.7	13.0	26.0–27.4	26.8	2.9–3.4	3.1
473–570 mm	2	37.9–41.0	39.5	11.9–12.1	12.0	24.9–25.1	25.0	3.5–3.6	3.6
P. aestuarius:									
37 mm	1		42.1		17.9		36.5		
66–81 mm	10	41.1–44.2	43.0	14.8–15.3	15.0	29.7–31.9	30.7	1.8–2.7	2.1
90–119 mm	12	41.6–44.9	42.7	13.6–14.6	14.2	28.1–30.3	29.4	1.7–2.5	2.0
125–203 mm	12	39.9–44.5	42.5	13.2–15.1	14.1	26.9–29.8	28.6	1.8–2.3	2.0
220 mm	1		44.5		14.2		29.6		3.0
330–381 mm	2	44.4–44.9	44.7	13.2–14.3	13.8	26.5–28.7	27.6	3.1–3.1	3.1
P. woolmani:									
48–57 mm	2	46.7–47.8	47.3	15.4–15.9	15.7	32.6–32.8	32.7		
72–105 mm	7	44.5–49.6	46.9	14.0–16.3	15.4	29.6–32.8	31.4	1.9–2.3	2.1
143–195 mm	4	44.6–48.7	46.4	14.2–15.3	14.9	29.5–31.4	30.3	2.2–2.7	2.4
232–258 mm	5	44.8–46.7	45.8	13.3–14.2	13.8	26.9–28.4	27.9	2.2–2.6	2.4
300–306 mm	2	45.8–47.9	46.9	13.7–14.0	13.9	27.5–28.0	27.8	2.7–3.0	2.9
429 mm	1		45.0		13.9		28.3		3.3
P. brasiliensis:									
131–214 mm	15	40.2–45.6	44.2	12.9–14.2	13.4	27.2–28.7	27.8	2.2–3.1	2.8
264 mm	1		44.4		12.5		25.1		2.9
477 mm	1		45.4		11.8		25.1		3.4
P. dentatus from Chesapeake Bay:									
29–49 mm	5	40.5–42.8	41.7	13.3–15.9	14.2	30.5–33.7	31.8		
64–92 mm	5	42.4–43.7	42.9	12.9–14.4	13.7	28.4–31.2	29.9	1.8–2.6	2.2
102–130 mm	6	40.8–44.7	43.7	12.5–14.2	13.6	27.2–29.8	28.5	1.6–2.2	1.9
159–194 mm	10	41.2–45.1	43.3	12.3–13.7	13.0	25.7–27.9	26.9	2.0–2.6	2.2
208–255 mm	10	41.1–44.0	42.6	11.7–13.9	13.1	25.4–27.5	26.6	2.1–2.8	2.5
300–390 mm	10	41.4–45.4	42.8	11.9–13.8	13.0	24.3–27.5	26.3	2.5–3.3	2.7
400–432 mm	2	42.0–42.6	42.3	13.1–13.9	13.5	26.6–27.6	27.1	3.1–3.3	3.2
P. dentatus from North Carolina:									
33–52 mm	4	41.8–46.5	44.2	14.3–14.9	14.5	32.1–33.4	32.9		
75–93 mm	5	42.9–45.8	44.1	13.2–13.8	13.5	28.2–30.9	29.5	1.2–2.3	1.8
98–130 mm	7	41.5–44.0	42.8	13.2–14.0	13.5	28.1–30.2	28.8	1.4–2.0	1.8
149–192 mm	9	[3] 41.5–45.0	43.7	13.3–15.0	14.0	27.1–29.2	28.5	1.6–2.3	2.1
208–253 mm	8	42.2–45.1	43.8	12.7–14.1	13.6	26.2–28.8	27.5	2.2–2.5	2.3
310–390 mm	10	40.3–45.6	42.4	12.9–14.6	13.3	25.7–27.8	26.5	2.1–2.9	2.5
427–441 mm	2	42.5–46.5	44.5	13.7–14.2	14.0	27.3–27.7	27.5	2.6–3.2	2.9
P. albigutta: [4]									
29–47 mm	10	42.2–44.6	43.4	15.2–17.4	16.3	32.8–35.0	34.0		
58–95 mm	10	[5] 41.7–46.2	44.4	14.7–16.7	15.6	30.1–33.4	31.5	1.9–2.7	2.3
102–130 mm	13	42.7–47.5	45.1	14.2–15.7	15.1	28.3–31.2	29.8	1.6–2.3	2.0
143–201 mm	[6] 16	41.9–46.9	43.6	14.6–16.8	15.8	[7] 28.3–31.1	29.7	1.8–2.8	2.2
207–273 mm	12	43.1–46.1	45.0	14.5–16.5	15.2	28.1–30.8	29.0	2.3–3.0	2.5
311–389 mm	7	39.3–44.5	41.7	14.1–16.7	15.5	27.5–30.5	28.7	2.7–3.6	3.1
P. lethostigma: [8]									
29–47 mm	8	40.8–44.3	42.6	15.3–17.4	16.0	32.4–34.3	33.4		
59–95 mm	7	39.8–43.6	41.5	14.7–17.2	16.1	29.5–32.2	31.0	1.7–2.9	2.2
111–132 mm	16	38.5–43.8	41.2	14.7–16.8	15.9	27.2–31.1	29.2	2.4–3.1	2.8
134–200 mm	11	40.8–45.5	42.6	13.2–16.2	15.3	26.5–29.8	28.5	2.6–3.6	3.1
206–292 mm	15	42.0–45.4	44.3	13.0–15.9	14.2	24.7–28.4	26.6	2.8–4.1	3.4
310–383 mm	8	43.6–46.7	45.2	13.9–15.0	14.4	25.8–27.3	26.7	3.4–4.1	3.9
393–472 mm	4	43.4–46.1	44.7	14.4–16.0	15.2	26.5–27.6	27.0	3.7–4.7	4.2
497–659 mm	4	45.2–47.7	46.2	14.1–16.2	15.2	25.7–28.6	27.4	4.0–5.2	4.6
P. squamilentus:									
30–45 mm	5	46.7–50.6	49.3	15.5–17.2	16.2	32.3–36.1	33.9		
96–120 mm	7	46.6–52.3	49.7	14.6–15.8	15.3	28.9–30.9	30.0	1.8–2.2	2.0
333–370 mm	4	49.7–52.1	50.7	13.2–13.6	13.4	26.8–27.4	27.1	2.1–2.8	2.6

[1] Head length from tip of snout to margin of opercle, not including the posterior soft border.

[2] Measured between soft margins.

[3] One specimen, 189 mm., unusually slender, depth 38.5. This measurement is not included in the average.

[4] Specimens measured from the following localities: Texas, 10 specimens, 29–47 mm., and 4, 58–68 mm.; Cedar Keys, Fla., 1, 308 mm; all others in a mixed lot from Beaufort, N. C., and Key West, Fla., the labels of many of them lost and not separable definitely. The somewhat irregular changes in proportional measurements with growth may be caused by the mixed samples, perhaps the number of specimens from each locality unevenly represented in the different categories.

[5] One specimen, 95 mm., having an unusually deep body, 49.3. This measurement is not included in the average. Specimen has 54 scales and a number of accessory scales, and is evidently not *squamilentus*. It has the typical color of *albigutta*.

[6] One specimen not included in this table, 148 mm., an extreme variant, unusually slender and with a notably long head and maxillary: depth 37.7; maxillary 17.7; head 32.4; interorbital 2.2.

[7] Another specimen, 154 mm., having an unusually long head for its size, 32.1. This measurement is not included in the average.

[8] Specimens from following localities measured and included in the table: in category 29–47 mm. are 8 specimens from Texas; 59–95 mm., 7 from Texas; 111–132 mm., 3 from Texas, and 13 from Louisiana; 134–200 mm., 1 from Texas and 10 from Louisiana; 206–292 mm., 4, 8, and 3 from Texas, Louisiana and North Carolina, respectively; 310–383 mm., 2, 2, and 4, from Texas, Georgia and North Carolina, respectively; 393–472 mm., 4 from North Carolina; 497–659, 2 from Texas, and 2 from North Carolina.

PROPORTIONAL MEASUREMENTS

In conventional taxonomic accounts of the species of *paralichthys* and related species a prominent part of the description is usually comprised of statements of the proportional measurements of various parts, while the statements referring to gill raker, fin ray and scale counts are apparently based on a few specimens; and such important characters as the structure of the scales, ctenoid or cycloid, and the presence or absence of accessory scales are often left out. However, for the purpose of distinguishing the species properly, proportional measurements are of secondary importance, except in a very few cases, the essential requisites being frequency distribution tables of the numbers of gill rakers, fin rays and scales, and descriptions of the typical structure of the scales and the presence or absence of accessory scales. In this investigation four measurements, the greatest depth, the length of the maxillary, the length of the head, and the interorbital width, were studied in detail, in order to test the practical value of these characters in the proper distinction of the species. The length of the pectoral differs as between *woolmani* and *brasiliensis*, and it may possibly show average differences between some other species. However, it was not investigated in detail, since after a cursory examination it was decided that it would not be of a more decisive nature than the other four measurements. In the genus *Hippoglossina* the upper eyeball and orbit were also measured, because these measurements are of some importance in separating the subgenera; while in the subgenus *Hippoglossina* the greatest width of the maxillary is of some importance in distinguishing the species.

There may be other measurements showing average differences between the species, but if there are any, they are apparently not pronounced. It was noted, as was to be expected, that the proportions of the parts investigated differ greatly with size, and the data were consequently separated by size groups. Indeed, the intraspecific differences due to size are frequently greater than the interspecific differences. The results of these measurements, segregated by size groups, are conveniently presented in tables 7 and 8. Summarizing the results, it may be stated that they are of some value, as follows.

The greatest depth is useful in separating *adspersus* from *californicus* and *aestuarius*. This difference is of no practical value in the identification of specimens because the former species is geographically discontinuous with the latter two and occurs in a widely separated region. However, since the other specific characters separating *adspersus* from the other two species are now shown to intergrade to a very large extent, the difference in the greatest depth is useful in proving their distinctness. The relative depth is also useful in aiding the separation of *squamilentus* from *lethostigma* and *dentatus*. In this case it is especially important to compare specimens of approximately the same size, and the depth is not the only important distinguishing character. Other characters show nearly as much divergence as the relative depth, although there is more or less intergradation in every one of those characters.

The relative length of the head and that of the maxillary are useful in separating *woolmani* from *brasiliensis*. While there is some intergradation in this character between the two species, the degree of overlapping is apparently less than in the other characters separating them. Here again it is necessary to compare individuals of approximately like size, and this character is of no practical value in the identification of specimens, the two species being discontinuous geographically, the former occurring on the Pacific coast and the latter on the Atlantic coast.

The interorbital width is useful in separating *lethostigma* from *dentatus* in specimens over 100 mm. long. In this case, also, it is necessary to compare individuals of approximately like size; while, on the other hand, the difference in the number of gill rakers distinguishes these two species readily.

Briefly then, of the proportional measurements investigated in detail, namely, the depth, head, maxillary, and interorbital, the depth of body is of value in aiding the separation of *squamilentus* and *adspersus* from related species; while the length of the head and maxillary is useful in presenting evidence that *woolmani* and *brasiliensis* are distinct species. *H. mystacium* may be distinguished from *H. stomata* by differences in the length and width of maxillary and the head length. In other species, differences in these measurements are of lesser importance.

CHANGE OF FORM WITH SIZE

In connection with an attempt to use the different body proportions for the proper distinction of the species, some interesting observations bearing on change of form with size have been made, which may be profitably discussed here. Of course, it was not the primary object of this investigation to study in detail the change of form with change in size, and an insufficient number of specimens were measured to describe with exactitude the form of the curves representing these changes. However, measurements made seem to justify certain conclusions which are of interest and importance in these flounders and may perhaps find a wider application. Since so much stress is laid on measurements in extant descriptions and they are of some use for the distinction of the species in a few cases, it is important to point out some of the changes noted with size. Some tentative conclusions suggested by a close scrutiny of tables 7 and 8 seem to be as follows.

The curve representing relative depth apparently follows a sinuous course during the life cycle of most species. That is, with growth it alternately increases and decreases, or vice versa, the change taking place more than once. Thus, in *aestuarius*, *woolmani*, and *lethostigma* there is a gradual decrease in depth in the smaller fish up to about 150 or 200 mm. After that length is reached it increases again. In *adspersus* and *albigutta* there is an increase in relative depth up to about 100 or 125 mm. and then it decreases as in the preceding three species, in fish up to about 200 mm. After that length is reached the depth increases in these two species also; but surprisingly, in *albigutta* the relative depth undergoes another change and the largest specimens become slender in comparison. In *dentatus* the alternate changes are apparently about the same as in *adspersus* except that they occur at a somewhat larger size. In *californicus* there is apparently a gradual decrease in relative depth from the smallest to the largest specimens.

These alternate changes in relative depth in most species may be due to changes in the rate of growth in length. That is, in the smaller fish there possibly is a marked acceleration in the tempo of growth in length which increases at a greater rate than the depth, the particular length at which this takes place differing with the species. With increase in size the accelerated growth in length slows up and the relative depth increases.

The head in young fish, those under 50 mm., is notably long in all species of *Paralichthys*. Its rate of growth soon slows down very markedly, and in somewhat larger specimens, about 50 to 70 mm., it becomes almost abruptly and palpably shorter in comparison with the standard length. It then continues to decrease slowly in relative length as the fish grows. In two species, *lethostigma* and *dentatus*, it appears to increase again in the largest specimens; but those measured are not in sufficient number to be certain of this, and the increase, if any, is moderate. Changes in the relative length of the maxillary with size, in general, follow that of the head length. The interorbital gradually increases in width as the fish grows.

In striking contrast to the species of *Paralichthys*, the head in *H. stomata* (table 7) increases gradually in relative length from the small to the large specimens. The depth in that species changes little with size.

It is evident that, with size, changes in the form of any part often differ markedly with the species. This is very important to bear in mind in connection with the use of measurements in distinguishing species. A difference between two species based on proportional measurements may hold at a given size, but not at other sizes. A striking case showing that a difference between two species may be reversed at a certain size is furnished by *lethostigma* and *albigutta*. Small and medium-sized specimens of *lethostigma* are more slender on the average than large specimens; but in *albigutta* the body evidently becomes more slender in large fish. As a result we have the interesting condition when comparing *albigutta* with *lethostigma* that the smaller specimens are relatively deeper in the former; but the proportions are reversed in large specimens, the former species being relatively more slender (table 8). The divergence between the two species with respect to depth is greater for the larger specimens.

It is to be noted that the length of the maxillary relative to the body length generally decreases in the larger specimens of *Paralichthys*. However, if the length of the maxillary is judged by the relation of its posterior extremity to the position of the eye, it seemingly increases with size, since its

hind margin reaches more and more posteriorly with respect to a vertical through the posterior margin of the eye, as the size of the fish increases. This is important to bear in mind, since species are sometimes distinguished on the basis of the position of the posterior margin of the maxillary with reference to the position of the eye. Again, the relation of the maxillary length is usually expressed as the number of times it enters into the head length. Since both the head and maxillary decrease relatively with size, at least up to a certain point, the numerical value of their ratio does not change much with the size, except in specimens under 50 mm. Anybody desiring to use this ratio may readily compute it by simple division of the averages given in the tables. However, this ratio does not always express specific differences, as for instance in the case of *woolmani* and *brasiliensis*. In these two species the measurement of the maxillary as compared with the standard length, shows a pronounced divergence; but when the maxillary length is compared with the head length the divergence disappears.

SPECIMENS AT THE BORDER LINE

Inspection of figures 1 to 4 afford sufficient proof that the three common eastern species are distinct. Since, however, there is often more or less intergradation when any single specific character is considered, it is of some importance and of considerable interest, to consider in greater detail how specimens at the border line were referred to their proper species in constructing the tables and graphs as presented in this report. After all, in identification it is individual fish that we are dealing with, and in such closely related species it is important that individual specimens are referred to other proper species.

First of all, it may be pointed out that the number of actually overlapping specimens are very few insofar as it relates to the counts of the gill rakers and the anal rays. In the case of the gill rakers (tables 3 and 4) there are no intergrading individuals between *dentatus* and *albigutta* or *lethostigma*. In the case of the anal rays (table 5) there would be no intergrades between *albigutta* and *lethostigma* or *dentatus* if only two individuals each of the latter two species are eliminated from the 381 specimens counted.

However, the number of actually overlapping specimens is not of primary interest. It is of greater interest to know, in such closely related species, just how all other specimens near the border line have been properly referred. For instance, two specimens having a total of 16 gill rakers have been referred to *dentatus*. What is the reason for placing them in that species and not in *albigutta*, since as far as the frequency distribution of that single character is concerned, it would be just as logical to refer them to the latter species (compare with table 4). Of these two specimens one has D. 89, A. 70, scales 67, and the other has D. 95, A. 71, scales 64. The color pattern is also that typical of *dentatus*. It is evident, therefore, that these other characters unmistakably remove these specimens from *albigutta*. They apparently belong to *dentatus* and are extreme specimens with respect to the gill-raker count. In the same way, other specimens at the border line with respect to any character may be referred with confidence to the proper species by at least one character falling outside the range of the most closely related species and at the mode or even the extreme outer end of its species.

Infrequently, no character is entirely decisive, but one character is sufficiently pronounced that the specimen may be placed with assurance. The following two fish from North Carolina are examples of such specimens. One has D. 83, A. 64; gill rakers 13+4, scales 63; the other, D. 80, A. 61, gill rakers 14+4, scales 59. They have ocellated spots, but the color pattern is somewhat intermediate between *dentatus* and *albigutta* and not typical of either species. It will be noted that in the anal ray count the former specimen is more like *dentatus* and the latter more like *albigutta*. The scales in the first specimen fall somewhat outside the range of *albigutta*, and considering also that the number of anal rays is just outside the range of that species, it would be more properly placed with *dentatus*. In the second specimen, the number of scales falls at the beginning or at the end of the frequency distributions of the two species, respectively. Both have been placed with *dentatus* largely on the basis of the gill-raker count. Reference to table 4 and figure 4 will show that this is the proper disposition of these two specimens.

After border-line individuals such as the preceding ones are placed, there remain a few speci-

mens none of the structural characters of which are decisively like their species. As examples of the latter, we may cite the case of two specimens from North Carolina here included with *albigutta*. One has D. 84, A. 63, the other D. 85, A. 62. The gill rakers in both are 10+2. It may be readily seen that so far as these characters are concerned, they may equally as well be referred to *lethostigma*. The number of scales is 54 and 53, respectively, this character being near the mode of *albigutta*, but it also falls at the extreme of variation of *lethostigma*. The two specimens, however, have the typical color pattern of *albigutta*, and it is evident that they are extreme specimens of that species with respect to the fin ray counts. A similar specimen from Cedar Keys, Fla. (U.S.N.M. 35085), likewise has all the structural characters examined close to the border line between *lethostigma* and *albigutta*, namely, D. 82, A. 63, gill rakers 2+11, scales 55, but the color pattern is strongly marked and, without a doubt, that of an *albigutta*. The last specimen is also of a size at which these two species show considerable differences in proportional measurements: length 376 mm.; depth 40.9; head 28.9; maxillary 15.3; interorbital 3. Comparing these measurements with those given in table 8 for specimens of similar size, it is found that they fall outside the range of *lethostigma*—the depth decidedly so—and within that of *albigutta*.

The preceding three specimens at the border line between *albigutta* and *lethostigma* showed the characteristic color pattern of the former sharply marked and could be placed with assurance in that species. The situation is more difficult when a similar border line specimen lacks ocellated spots. The question then may arise: Is it a *lethostigma* because of the lack of such spots, or is it an individual variant of *albigutta* with respect to color, since occasional specimens of the latter species, especially dark individuals, have the spots very faint? One such specimen from North Carolina was examined: it has D. 81, A. 63, scales 57, total number of gill rakers 12, and lacks ocellated spots. Every one of these important structural characters is about intermediate between *albigutta* and *lethostigma* and characteristic of neither species. The color is like *lethostigma*, but it may possibly be an individual variant of *albigutta*. This specimen, 330 mm. long, was placed with *lethostigma* on the basis of its proportional measurements, namely, depth 46.5, head 27.1, interorbital 3.4. Comparing these measurements with those given in table 8 for the group of specimens of similar size, it may be seen that the depth falls decidedly outside the range of *albigutta* and near the outer extreme of *lethostigma*. The head measurement also falls within the range of *lethostigma* and outside that of *albigutta*, but very near that of the latter. The color agrees with that of *lethostigma*.

By following the methods outlined, it was thus possible to place individual fish near the border line with their respective species. Out of a total of nearly 400 specimens studied in detail, only one was found, the last one described, about which some shade of doubt exists, and this is because specimens of similar size were not available in sufficient number to determine with entire assurance the difference in measurements. Even assuming that it is a doubtful specimen—which it hardly is—the proportion of doubtful specimens, one out of nearly 400, is low, probably less than is usually the case among closely related species.

It may be suggested that this last specimen is a hybrid, but this would be a mere assumption although within the realm of possibility. While some of the border-line specimens discussed in the preceding paragraphs may possibly be hybrids (p. 321), it would be necessary to make a much more detailed study to be able to identify any hybrid specimens with reasonable assurance. At any rate, it seems evident that hybrid specimens of these flounders, if present, are comparatively few in nature. The above placement of the border line specimens apparently is in accord with their specifically genotypic origin, except a very few possible hybrids, the existence of which it is not possible to prove definitely at present.

While the three common eastern species may be distinguished readily even to individual fish, soon after the rays and gill rakers become differentiated, in fish of about 15 mm., this is not the case with two common and geographically adjacent species of the west coast, namely, *californicus* and *aestuarius* (p. 308). Small specimens, up to about 175 mm., of these two species are sometimes not possible to place with confidence. The two west coast species differ also in the frequency distributions of the numbers of fin rays, but there is more inter-

gradation than in the eastern species, and furthermore, in the case of small specimens of the west coast species, there are no characters which may be correlated with the fin ray count, the number of gill rakers and scales and the color being nearly alike in those two species.

GENERIC LIMITS

External characters altogether satisfactory for the division of the species treated in this paper into major groups or genera have not been proposed hitherto. None were elaborated during the present investigation, except one which although not entirely satisfactory is apparently more so than those hitherto proposed. These characters are discussed in reverse order of their apparent importance.

The presence of an anterior accessory branch of the lateral line has been used for distinguishing *Pseudorhombus;* but this is the least important of all characters and is of very little usefulness in generic division. This character and the number of vertebrae are discussed at greater length on page 298.

The structure of the scales, cycloid or ctenoid, is of some moderate use. The known species which apparently belong to *Paralichthys* either have all scales cycloid or when ctenoid scales are present they are typically confined to the eyed side. Sometimes very few ctenoid scales are present on the blind side as a rather infrequent individual variation. If a species typically does have ctenoid scales on the blind side, it is highly probable that it does not belong to *Paralichthys*. In the known species of *Hippoglossina* ctenoid scales are either present on both sides or absent on both sides. In the known species of *Pseudorhombus* the scales are ctenoid on the eyed side and ctenoid or cycloid on the blind side. This character is useful for subgeneric division. The species of *Paralichthys* may be divided into two apparently natural groups by the presence or absence of ctenoid scales on the eyed side. In *Pseudorhombus* the same difference on the blind side may possibly be used for subgeneric division. In one subgenus of *Hippoglossina*, however, this difference is only of specific importance.

The structure of the scales is very constant intraspecifically with two exceptions. In *H. oblonga* the number of ctenoid scales differs greatly with the individual (p. 294). In *P. aestuarius* the ctenoid scales lose their spinules with growth and all scales are cycloid in large specimens. However, in spite of the relative constancy of this character it is of limited use for generic division. It is evident that the disappearance of ctenoid scales occurred independently in all three genera. (The presence of cycloid scales appears to represent a more recent development in the species concerned.) Consequently, to use this character by itself for the major division of the species into genera would run counter to their natural relationship and lead to the formation of polyphyletic genera.

The size of the eye and the interorbital width are of importance in separating the species placed in *Hippoglossina*, but the transition between extreme species in these respects is rather gradual. The same is true of the size of the teeth. The species placed in *Paralichthys* have markedly long, fanglike teeth, while those placed in *Hippoglossina* have rather small teeth; but here also there is a gradual transition, some of the species placed in *Pseudorhombus* having the teeth intermediate in size. No sharp lines may be drawn between the major groups, or genera, on the basis of these three characters.

The position of the dorsal origin is of considerable importance. In the species of *Hippoglossina* the dorsal begins approximately over the middle of the eye, while in nearly all other species it begins over the anterior margin of the eye or a little more forward. However, this character does not separate all the species. In *microps* (p. 301) which, judged by other characters, apparently belongs to *Paralichthys*, the dorsal origin is over about the middle of the eye.

The presence or absence of accessory scales was found to be a good criterion for the generic separation of the species concerned. All the species of *Hippoglossina* examined lack accessory scales. All those of *Paralichthys* have such scales. (They are very few in *squamiltentus*, p. 333). The following exotic species of *Pseudorhombus*, labeled as such or under their synonyms in the National Museum, were examined for this character, namely, *arsius*, *javanicus*, *jenynsii*, *pentophthalmus*, *cinnamoneus*, *oligodon* and *oligolepis* (Norman, Monogr., 1934). These identifications were made by a number of previous workers from time

to time, but their authenticity was not checked. All the numerous specimens examined lacked accessory scales. Of the American species, *isosceles* lacks accessory scales and it is apparently a *Pseudorhombus* (p. 299); but in the species described as *Paralichthys triocellatus* by Miranda Ribeiro, which is possibly also a *Pseudorhombus*, this character may vary with individual fish (p. 335).

The accessory scales appear rather late in the life of the fish and this character is probably a late evolutionary acquisition. In *P. dentatus* and *P. albigutta* they appear only after the fish has attained a length of about 75–90 mm., and in these two species they seem to develop at a smaller size than in the others. In *P. brasiliensis* they seem to develop first in specimens between 130 and 155 mm. On account of their late appearance the practical usefulness of this character is limited. The relative development of this character also differs much with the species. For instance, the accessory scales are profuse in large specimens of *dentatus* and *albigutta*, while in *brasiliensis* they are rather few in number. This character, therefore, is seemingly also not of transcendent importance in generic separation.

This character was neglected by authors in general and it is difficult to appraise its true value. Norman (Monogr., p. 46, 1934) states: ". . . the presence of supplementary scales . . . provide features of taxonomic importance." He includes this character in the definition of some genera but fails to mention it in others. Later, in discussing *Paralichthys isosceles*, Norman (Disc. Rept. vol. 16, p. 135, 1937) states: ". . . I am not convinced of the value of this character [the absence of supplementary scales] in the definition of genera." However, irrespective of the value of this character in the family as a whole, it is evident that in the species concerned it is of at least as much value as the other character employed in the delimitation of genera. Judged by the species studied by me, it seems likely that it will prove to be of greater value than the other characters for the major divisions of the species, in showing relationship and in the separation of genera. Of course, a final solution of the question must wait until this character is determined in all the species involved, its development with size, and its individual variability, especially in *triocellatus* which possibly forms an exception.

The foregoing consideration of the generic characters makes it evident that the three genera as now constituted are not sharply distinguished. With the possible exception of the accessory scale character, no other single character will delimit any one of the three genera concerned. The delimitation of the genera depends rather on a combination of characters and the lines drawn between them are more or less arbitrary. As far as our present knowledge of the morphology of the species studied is concerned there are substantial reasons for placing them in a single genus, *Paralichthys*, divisible into a number of subgenera. However, they evidently form groups of related species and in view of the comparatively large number of species involved, it is desirable to split them up into convenient genera. Another cogent reason for adopting this course is that by doing so the current nomenclature of the species will be least disturbed. It is also possible that a further, intensive study of the species will reveal satisfactory internal characters to separate the genera.

KEY TO AMERICAN SPECIES OF HIPPOGLOSSINA, PSEUDORHOMBUS, AND PARALICHTHYS [3]

A. Accessory scales absent in large as well as small fish.[4] Anterior teeth only slightly or not enlarged, sometimes moderately enlarged.

B. Origin of dorsal behind anterior margin of eye; eyeball and orbit very large to moderately large; interorbital reduced to a mere ridge; the three characters occurring together. Accessory branch of lateral line rather poorly developed, not reaching dorsal profile. Ctenoid scales either present on both sides or absent on both sides. Most prominent spots either 4 or 6, depending on the subgenus, in two longitudinal rows, occupying nearly the same positions in all the species; prepeduncular spot obsolescent or absent ..... genus *Hippoglossina* (p. 287)

a. Orbit and eyeball strikingly large, 10.4 to 12.1 and 7.3 to 9.6, respectively, in large specimens. Origin of dorsal usually over or nearly over middle of eye in large as well as in small specimens. Preanal spine (first interhaemal) usually well developed and visible externally. Typical color pattern with 6 prominent spots, incompletely ocel-

[3] Species of which no specimens were examined are placed in brackets. See also p. 334 for three species of doubtful relationship and position.

[4] Small specimens of all the species lack accessory scales, have a narrow interorbital, a comparatively large eye, and the dorsal origin is more or less behind the anterior margin of the eye. Consequently, this key should be used with care in placing small specimens.

lated. Scales 45 to 56. Anal rays 46 to 55. Dorsal rays 60 to 70. Ctenoid scales present on both sides. Anterior teeth hardly enlarged_____subgenus *Hippoglossina* (p. 288)

b. Ctenoid scales on blind side extending forward to middle of body or more anteriorly. Depth 42.4 or less.

c. Entire number of gill rakers on first arch 11 to 13. Ctenoid scales on blind side usually extending nearly to shoulder girdle, varying to about a vertical through middle of arch. Maxillary with 3 to 6 cycloid scales. Dorsal rays 60 to 65. Anal rays 46 to 51. Depth 34.8 to 38.3; length and width of maxillary 13.7 to 14.9 and 3.2 to 3.7, respectively; head 30.8 to 32.8 (6 specimens 140 to 167 mm. measured).

Hippoglossina (*Hippoglossina*) *bollmani* (p. 288)

cc. Entire number of gill rakers on first arch 15 to 21. Ctenoid scales on blind side usually not extending forward of posterior angle in lateral line, varying to about a vertical through middle of arch. Dorsal rays 63 to 70. Anal rays 47 to 55. Depth 36.8 to 42.4.

d. Three cycloid scales on maxillary. Length and width of maxillary, 13.6 and 3, respectively; head, 30.7 (1 specimen 183 mm. measured). Coast of Chile_____*Hippoglossina* (*Hippoglossina*) *mystacium* (p. 289)

dd. Maxillary with a small patch of 7 to 16 scales, all or at least some of them ctenoid. Length and width of maxillary 14.6–16.1 and 3.6–4.2, respectively; head 31.5–33.7 (range of 7 specimens 138–208 mm.). Coasts of California and lower California_____*Hippoglossina* (*Hippoglossina*) *stomata* (p. 289)

[bb. Ctenoid scales on blind side present only on posterior third. Depth 43–45.

Hippoglossina (*Hippoglossina*) *macrops*] (p. 291)

aa. Orbit rather large, 7.4 to 9.3 in large specimens; eyeball 6.1–7.6 in large specimens. Origin of dorsal usually over space between anterior margin of eye and that of pupil in large specimens, nearly over middle of eye in small fish. Preanal spine covered by skin, not visible externally. Typical color pattern with 4 very prominent ocellated spots. Scales, 63–81. Anal rays, 58–72. Dorsal rays, 72–86_____subgenus *Lioglossina* (p. 293)

e. Ctenoid scales present on both sides, their number highly variable (p. 294), but at least a few alway spresent on head of eyed side and caudal peduncle of blind side. Anterior teeth very moderately enlarged. Anterior two spots on a vertical nearer to head than base of caudal. Atlantic.

Hippoglossina (*Lioglossina*) *oblonga* (p. 293)

ee. Scales all cycloid on both sides. Anterior teeth but slightly enlarged. Anterior two spots on a vertical about midway between posterior margin of head and base of caudal. Pacific.

Hippoglossina (*Liaglossina*) *tetrophthalmus* (p. 297)

BB. Origin of dorsal over or in front of anterior margin of eye; eyeball and orbit varying from comparatively small to rather large; interorbital varying from medium width to a mere ridge. Accessory branch of lateral line rather well developed, usually, but apparently not always, reaching dorsal profile. Ctenoid scales present on eyed side (except possibly in *tenuirostrum* (Norman Monogr., p. 95), present or absent on blind side depending on the species. Color pattern differing with the species, prepeduncular spot prominent in some. Includes one American species, *isosceles* (p. 299), possibly also *triocellatus* of Miranda Ribeiro (p. 334)_____*Pseudorhombus* (p. 298)

AA. Accessory scales present (very few in *squamilentus*); usually beginning to develop on the fish reaching a length of about 75 to 150 mm.; their first appearance with respect to length differing with the species and to some extent with individual fish. Anterior teeth strongly enlarged in most species, caninoid, sometimes moderately enlarged, never subequal. Eye rather small. Most prominent spots usually forming a triangle including the prepeduncular spot.

Paralichthys (p. 300)

f. Scales on eyed side ctenoid, at least in fish up to about 160 mm.[5]_____ subgenus *Paralichthys* (p. 301)

[g. Origin of dorsal nearly on a vertical through middle of eye. Gill rakers on lower limb 18 to 23.

Paralichthys (*Paralichthys*) *microps*] (p. 301)

gg. Origin of dorsal approximately over anterior margin of eye, except in the young.

h. Gill rakers on lower limb not more than 11.

i. Dorsal of blind side not spotted. Pectoral approximately 2 in head.

j. Pectoral rays 12. Scales 76. Sinistral. Atlantic_____ *Paralichthys* (*Paralichthys*) *patagonicus* (p. 301)

[jj. Pectoral rays 11. Scales 62. Dextral. Pacific_____ *Paralichthys* (*Paralichthys*) *hilgendarfii*] (p. 304)

ii. Dorsal of blind side spotted. Pectoral 2.3 to 2.4 in head. Sinistral.

k. Scales 68. Gill rakers on lower limb 9_____ *Paralichthys* (*Paralichthys*) *schmitti* (p. 305)

[kk. Scales 94. Gill rakers on lower limb 11_____ *Paralichthys* (*Paralichthys*) *fernandezianus*] (p. 305)

hh. Gill rakers on lower limb not less than 15.

l. Depth 44–48 and scales ctenoid in large as well as in small specimens. Sinistral. Total number of gill rakers 22–27. D. 68–76. A. 54–61. Pacific Coast of South America.

Parolichthys (*Paralichthys*) *adspersus* (p. 306)

ll. Depth 37–45, when more than 43.5 (in *aestuarius*) scales becoming cycloid with growth. Very often dextral.

m. Scales retaining their ctenoid character at all ages. Dorsal rays 66 to 76. Anal rays 49 to 59. Total

[5] In *aestuarius* the scales lose their ctenoid character on reaching a length between 160 and 220 mm. Larger specimens of this species may be separated from others having cycloid scales by the many gill rakers, 24 or more in total number. In very large specimens of some other species the spinules on the scales may change to coarse granular asperities, but their early ctenoid condition and distinguishing nature is still evident.

number of gill rakers 25 to 32, the greatest concentration of individuals at 28 to 29. Depth 37 to 43.5. California and west coast of lower California ..... *Paralichthys* (*Paralichthys*) *californicus* (p. 307)

mm. Scales becoming cycloid with age (the change from ctenoid to cycloid scales taking place in fish between 160 and 220 mm.) Dorsal rays 75 to 85. Anal rays 57 to 67. Total number of gill rakers 24 to 31, the greatest concentration at 27 and 28. Depth 40 to 45. Gulf of California and west coast of Lower California ..... *Paralichthys* (*Paralichthys*) *aestuarius* (p. 310)

ff. Scales without spinules at all ages ..... subgenus *Chaenopsetta* (p. 312)

n. Gill rakers on lower limb of first gill arch 13 or more (except *woolmani* from the Pacific occasionally having 12 or 11).

o. Anal rays 54 to 60. Dorsal rays 68 to 81. Total number of gill rakers 17 to 21 in nearly all specimens, varying 16 to 22.

p. Head 29.5 to 31.4; maxillary 14.2 to 15.3; depth 44.6 to 48.7 (in 4 specimens 143 to 195 mm.). Pectoral rays predominantly 12, often 11; pectoral of eyed side usually reaching lateral line. Origin of dorsal usually over anterior margin of eye in medium-sized specimens. Pacific coast ..... *Paralichthys* (*Chaenopsetta*) *woolmani* (p. 312)

pp. Head 27.2 to 28.7; maxillary 12.9 to 14.2; depth 39.8 to 45.6 (in 15 specimens 131 to 214 mm.). Pectoral rays predominantly 11, sometimes 10 on one or both sides; pectoral of eyed side usually falling short of lateral line. Origin of dorsal in medium-sized as well as large fish more or less in front of anterior margin of eye. Atlantic coast of South America ..... *Paralichthys* (*Chaenopsetta*) *brasiliensis* (p. 314)

oo. Anal rays 61 to 73. Dorsal rays 80 to 96. Total number of gill rakers nearly always 20 to 24, varying 16 to 24. Pectoral rays predominantly 12. Atlantic coast of the United States.

Paralichthys (*Chaenopsetta*) *dentatus* (p. 316)

nn. Gill rakers on lower limb not more than 12. Atlantic.

q. Scales in not more than 60 rows over straight part of lateral line. Anal rays not more than 63.

r. Pectoral rays predominantly 11, varying 10 to 12. Ocellated spots present. East coast of United States.

Paralichthys (*Chaenopsetta*) *albigutta* (p. 324)

rr. Pectoral rays 10. No well-marked ocellated spots. Brazil ..... *Paralichthys* (*Chaenopsetta*) *vorax* (p. 327)

qq. Scales usually in more than 60 rows; when less (in *lethostigma*) anal rays nearly always 64 or more (63 in 2 specimens of *lethostigma* out of 153).

s. Body moderately deep, not more than 43.8 in specimens 59 to 132 mm. (23 *lethostigma* measured), not more than 46.7 in specimens 134 to 472 mm. (36 *lethostigma* and 1 *tropicus* measured). Entire number of gill rakers on first arch 10 to 13. Accessory scales in rather moderate numbers or profuse.

t. Anal rays 58. Dorsal rays 75. Vertebrae 10+26. Interorbital 2.2. Accessory scales profuse (1 specimen 321 mm. studied). Trinidad ..... *Paralichthys* (*Chaenopsetta*) *tropicus* (p. 327)

tt. Anal rays 63 to 77. Dorsal rays 80 to 95. Vertebrae 10 to 11+27 (in 2 specimens). Interorbital 3.4 to 4.1 (in 8 specimens 310–383 mm.). Accessory scales usually in moderate numbers. East coast of United States ..... *Paralichthys* (*Chaenopsetta*) *lethostigma* (p. 328)

ss. Body notably deep, 46.6 to 52.3 in specimens 96 to 120 mm. (7 measured); 49.7–52.1 in specimens 333 to 370 mm. (4 measured). Entire number of gill rakers 13 to 16. Accessory scales very few. Anal rays 59 to 64. Dorsal rays 76 to 82. Vertebrae 10+28 (in 1 specimen). East coast of United States.

Paralichthys (*Chaenopsetta*) *squamilentus* (p. 332)

HIPPOGLOSSINA

This genus is distinguished from *Paralichthys* (for definition see p. 300) and *Pseudorhombus* chiefly by the following combination of characters. Accessory scales absent. Origin of dorsal on space over pupil. Interorbital reduced to a mere ridge in large as well as in small specimens. Eye large. Teeth small. Scales either ctenoid on both sides or cycloid on both sides. Accessory branch of lateral line rather poorly developed, not reaching dorsal profile. Prepedunecular spot obsolescent; most prominent spots 4 or 6, depending on the subgenus, in two longitudinal rows. This genus is divisible into two subgenera.

The boundary between *Hippoglossina* and *Paralichthys* is not sharp. The accessory scales are sparse in some species of *Paralichthys*. In the dorsal origin and in the size of the eye and the teeth, the subgenus *Lioglossina* is rather intermediate between *Paralichthys* and the typical subgenus of *Hippoglossina*. One or two species of *Paralichthys* have a backward insertion of the dorsal (p. 301). One species, *coeruleosticta* (p. 335), apparently shows a combination of a number of characters common to both genera. However, the contained species apparently form, on the whole, two fairly distinct though not sharply divergent groups. But, if the two groups of species are recognized as distinct genera, *oblonga* which has been placed in *Paralichthys* by all recent authors must be placed in *Hippoglossina*.

Hippoglossina is even nearer to *Pseudorhombus*, both genera agreeing in the absence of accessory scales. They differ slightly in the origin of the

dorsal, over anterior margin of pupil or a little more backward in *Hippoglossina*, over anterior margin of eye or a little more forward in *Pseudorhombus*. The typical subgenus of *Hippoglossina* diverges in a more pronounced manner from *Pseudorhombus* in this respect, but the subgenus *Lioglossina* is rather intermediate. The accessory branch of the lateral line is poorly developed in *Hippoglossina;* it is usually well developed in *Pseudorhombus* reaching the dorsal profile in most, but apparently not in all the species. The interorbital is reduced to a mere ridge in *Hippoglossina;* in most species of *Pseudorhombus*, but apparently not in all, it is wider than a mere ridge. The eye in the typical subgenus of *Hippoglossina* is markedly large, but in the subgenus *Lioglossina* it is nearly the same as in some species of *Pseudorhombus*. In *Hippoglossina* ctenoid scales are present on both sides or absent on both sides; in *Pseudorhombus* ctenoid scales are present on the eyed side and present or absent on the blind side. No other characters than the foregoing are now known by which the two genera may be distingnished. They are hardly adequate as generic characters, and the separation of the two genera is now largely a matter of convenience.

Subgenus Hippoglossina

Hippoglossina Steindachner, Sitzb. Akad. Wiss. Wien 74 (1): 161 (Ichthy. Beit. 5: 13) 1876 (genotype *Hippoglossina macrops* Steindachner by monotypy).

A comparative discussion of the differences between this subgenus and *Lioglossina* is given under the latter (p. 293). The four known species of this subgenus are confined to the Pacific Coast of North and South America, in rather deep water.

HIPPOGLOSSINA BOLLMANI

(PLATE 1)

Diagnosis.—Scales on eyed side ctenoid on head and body; on blind side cycloid on head, ctenoid on body, the ctenoid scales extending forward to within 3 to 8 rows of gill opening, sometimes to about a vertical through middle of arch in lateral line. Maxillary of eyed side with 3 to 6 cycloid, more or less embedded scales, usually in one row, sometimes in two irregular rows. Scales 45 to 49. No accessory scales. Gill rakers 11 to 13 in total number; 2 or 3 on upper limb; 9 or 10 on lower. Anal rays 46 to 51; dorsal rays 60 to 65. Pectoral rays on eyed side usually 11 (in 5), sometimes 10 (in 1): on blind side usually 10 (in 5), sometimes 11 (in 1). Origin of dorsal very nearly over middle of eye (specimens 140—167 mm. examined). Teeth nearly equal, the anterior ones slightly enlarged. Maxillary extending to a vertical through middle of eye or posterior margin of pupil. Eye conspicuously large; body slender; head and maxillary of medium length. Sinistral.

Color.—Specimens examined faded. Six conspicuous spots evident, 3 in a longitudital row below dorsal profile and a similar row above ventral profile, nearer to profiles than to a median line. Smaller spots evident on caudal peduncle, one each at base of caudal rays, at upper and lower angles, continued on blind side. A row of small white spots close to dorsal profile, and a similar row at ventral profile. Margins of caudal, dorsal and anal on blind side, blackish posteriorly.

Specimens examined and geographic distribution.—Panama Bay; Albatross Station 2805; lat. 07°56′ N., long. 79°41′30″ W.; 51.5 fathoms; March 30, 1888 (41143, the type; 41147, 41156, 41187, 41216, 41250). Number of specimens studied 6, 140 to 167 mm. Jordan and Bollman (1889) state on page 176, "Numerous specimens were dredged at station 2805," and on page 183 they record it from station 2804 as well. The latter station is a little north and east of 2805, namely, lat. 08°16′30″ N., long. 79°37′45″ W., 47 fathoms; but no specimens from that station are now present in the U. S. National Museum.

Distinctive characters and relationship.—This species differs from *stomata* chiefly in the smaller number of gill rakers as pointed out under the latter (p. 291), where the other characters distinguishing the two species are also discussed. Its relationship to *mystacium* and to *macrops* is discussed under the latter two species (pp. 289 and 292). What may prove to be a unique feature of this species is that the number of pectoral rays on the blind side is predominantly one less than on the eyed side. In all species of *Paralichthys* the numbers are predominantly the same on both sides, while *H. stomata* is rather intermediate in that respect.

Hippoglossina macrops Jordan and Bollman (not Steindachner), Proc. U. S. Nat. Mus. 12: 175, 1889 (Albatross Station 2805).—Jordan and Bollman, ibid., p. 183 (recorded from Albatross Stations 2805 and 2804).

Hippoglossina bollmani Gilbert, Proc. U. S. Nat. Mus. 13: 123, 1890 (based on Jordan and Bollman's account).—

JORDAN and EVERMANN, Bull. U. S. Nat. Mus. 47 (3): 2621, 1898 (No. 41143 designated as type).

Hippoglossina vagrans GARMAN, Mem. Mus. Comp. Zool. 24: 221, 1899 (off the coast of Colombia, 66 fath.; the structural characters given in original description agree with *bollmani*, but color somewhat different; needs further investigation).

Hippoglossina bollmani MEEK and HILDEBRAND, Field Mus. Nat. Hist. Chicago (zool. ser.) 15 (3): 973, 1928 (compiled account).—NORMAN, Monogr. Flatfishes, p. 68, fig. 36, 1934 (reviewed).

HIPPOGLOSSINA MYSTACIUM

Diagnosis.—Scales on eyed side ctenoid on body, mostly cycloid on head, but many weakly ctenoid scales present; on blind side ctenoid scales present on posterior part of body, extending on midline to a distance behind arch about equal to half its chord, scales on head and on body anteriorly cycloid. Maxillary with 3 cycloid embedded scales in one row. Scales 52; 28 perforate scales in arch. Accessory scales absent. Gill rakers 3 comparatively long ones on upper limb, with 2 widely spaced and very small ones above; 12 on lower limb. Anal rays 55; dorsal rays 66. Pectoral rays 11 on eyed side, 10 on blind side. Origin of dorsal nearly over middle of eye. Anterior teeth but slightly enlarged. Maxillary extending to a vertical through posterior margin of pupil. Eye notably large; body rather slender; head and maxillary short, the maxillary conspicuously narrow distally. Sinistral.

Color.—Nearly faded; traces of 6 spots in 2 lengthwise rows present, as in other species of the subgenus, somewhat nearer to upper and lower profiles than to straight part of lateral line; every spot in either row placed on a transverse line with its fellow in the other row, first pair of spots on a transverse line through about middle of arch in lateral line, second pair on a vertical somewhat nearer to head than to base of caudal, third pair not far from ends of dorsal and anal fins; traces of smaller spots on caudal peduncle, near upper and lower posterior angles, at base of caudal rays, these two spots being continued to a slight extent on blind side.

Specimen examined and geographic distribution.—The above account is based on the type specimen (77393) 183 mm., taken near Taita Peninsula, Chile; Albatross Station 2787, 46°47′30″ S, 75°15′ W; in 61 fathoms. The two specimens examined by Günther and by Norman (see synonymy) extend the range of this species to the Straits of Magellan.

Distinctive characters and relationship.—In the number of gill rakers and dorsal and anal rays, the single specimen studied is more like *stomata* than *bollmani*. The extent of ctenoid scales on the blind side is less than in most specimens of *stomata*, but some individuals of the latter species approach *mystacium* closely. The ctenoid scales on the eyed side of the head are fewer, and in general, the ctenoid character of the scales is weaker than in *stomata*, but there is considerable variation in those respects in the latter species. A striking difference shown by the type specimen which attracts immediate attention is the narrow maxillary. This species also has a shorter head and maxillary than *stomata* (table 7). It further differs from *stomata* in having fewer scales on the maxillary, which are cycloid instead of ctenoid.

This species is apparently more remotely related to *bollmani*. It differs from the latter which occurs nearer to its range, in having more numerous gill rakers and dorsal and anal rays and in the ctenoid scales not extending so far forward. It agrees with *bollmani* in having cycloid scales on the maxillary. In the number of scales on the maxillary, the length and width of the maxillary and the length of the head, *mystacium* will most probably be found to intergrade with *bollmani*.

As compared with the original description of *macrops*, this species differs in having a more slender body, a shorter head, and the ctenoid scales on the blind side evidently extend more forward.

Hippoglossina macrops GÜNTHER, Proc. Zool. Soc. London 1881: 21 (Trinidad Channel, listed).—Thompson, Proc. U. S. Nat. Mus. 50: 424, 1916 (specimen from off Taita Peninsula forming type of *mystacium*).—NORMAN, Monogr. Flatfishes, p. 67, 1934 (account based on specimens recorded by Günther).

Hippoglossina mystacium GINSBURG, Jour. Washington Acad. Sci. 26: 130, fig. 1, 1936 (based on specimen recorded by Thompson).—Norman, Disc. Rep. 16: 132, 1937 (identification of specimens from Trinidad Channel corrected).

HIPPOGLOSSINA STOMATA

(PLATE 2)

Diagnosis.—Eyed side having nearly all scales on body ctenoid, those on head variable, usually nearly all ctenoid, sometimes the majority cycloid, but some ctenoid scales always present; on blind

side cycloid on head, ctenoid on greater posterior part of body, the ctenoid scales usually extending on midline to about posterior end of arch, in lateral line, varying with individual fish, with that point as a center, from a vertical about through the middle of the arch to an equal distance behind; broad wedge shaped areas of cycloid scales usually extending backward above and below the median ctenoid scales for variable distances, sometimes the ctenoid scales ending everywhere on the same, nearly straight, transverse line (above description applying to specimens 116 mm. or more; in two small specimens, 54 and 55 mm., ctenoid scales present only on posterior half of body, the spinules probably not having as yet developed on the more anterior scales: compare with account of *oblonga*, p. 294). Maxillary of eyed side with a small patch of 7 to 16 scales, usually in 3, sometimes in 2 or 4 irregular rows, all or nearly all ctenoid in medium-sized specimens (116–208 mm.) with the spinules rather well developed, sometimes a few of them cycloid; in larger specimens (240–313 mm.) most of them apparently cycloid but early ctenoid nature of a few at least always evident by rather weak spinules or granular asperities (in 2 specimens 54 to 55 mm. scales on maxillary rather small, cycloid and embedded apparently not far from beginning of development). Scales 45 to 56; accessory scales absent. Gill rakers on first arch modally 18 in total number, varying 15 to 21; 4 or 5, sometimes 6 on upper limb; modally 13 on lower limb, varying 11 to 15. Anal rays 47 to 55; dorsal rays 63 to 70. Pectoral rays nearly always 11 on eyed side (in 12 specimens), sometimes 12 (in 1); on blind side 10 (in 5), or 11 (in 8). Origin of dorsal very nearly over middle of eye in small and also large specimens, sometimes nearer to anterior margin of pupil than middle of eye in large fish. Teeth nearly equal, the anterior ones slightly enlarged. Maxillary extending to a vertical through middle of eye in 2 specimens 54 and 55 mm., generally to posterior margin of pupil in specimens 116 to 208 mm., to about posterior margin of eye or below the space between the posterior margin of pupil and posterior margin of eye in specimens 240 to 334 mm. Eye conspicuously large; depth medium; head and maxillary long, gradually increasing in length with growth up to largest specimens (compare with discussion on page 281). Sinistral.

Color.—Most specimens examined are faded, where color is present it may be described as follows: Ground color a light brownish yellow, irregularly speckled with darker; many ring-like spots of a dark brown on body and head, often the inside area of the ring becoming more or less pigmented like the periphery, except a small area near the margin, thus forming a rounded dark spot with a small lighter area on one side, the lighter area sometimes in form of a short curved band, the spot then suggesting an incomplete ocellus; 6 spots especially conspicuous and persisting in nearly all faded specimens, forming a longitudinal row of three spots below dorsal profile and a similar row over ventral profile; the pair of anterior spots usually less prominent than other 4 on a transverse line dividing an imaginary chord of the arch into two unequal parts, about three-fifths anteriorly and two-fifths posteriorly; middle pair of spots on a vertical somewhat nearer to head than base of caudal; posterior pair of spots near ends of vertical fins, extending partly on the fins. A pair of smaller spots on caudal peduncle, one above and one below, at base of caudal rays, more or less evident, these spots continued for a short distance onto blind side. Caudal of blind side, and to a lesser extent also anal and dorsal, shaded with dark in some specimens. In the two smallest fish, 54 and 55 mm., a faint lighter bar, bordered faintly with a diffuse darker pigmentation extending across the fish between each of the posterior two pairs of spots. The color in life, according to Eigenmann, is strongly tinged with blue, with numerous spots of light blue and with five pairs of dark brown ocelli, the alternate ones more conspicuous. The latter spots are evidently those which persist in preserved specimens, but their ocellate character disappears or becomes faint after preservation.

Lectotype.—Two specimens were described by Eigenmann without designating a holotype. One of these, U.S.N.M. 41905, 315 mm. in total length, is hereby designated as the lectotype.

Specimens examined.—Santa Barbara Channel, off Santa Barbara, Calif.; Albatross Station 2961; lat. 34°22′45″ N. long. 119°40′30″ W; 21 fathoms; Feb. 11, 1889 (47289). Santa Barbara Channel, off Ventura, Calif.; Albatross Station 2971; lat. 34°20′23″ N. long. 119°37′50″ W; 29 fathoms; Feb. 11, 1889 (46324). Nearly same position as

preceding: Albatross Station 2970; lat. 34°20′20″ N. long. 119°37′30″ W; 29 fathoms; Feb. 11, 1889 (46420). Off Avalon, Dakins Cove, Santa Catalina I., Calif., Albatross Stations 3662 and 3663; 47 fathoms, April 8, 1897 (77967). San Pedro Channel, Calif.: Albatross Station 2939; lat. 33°36′ N. long. 119°09′30″ W; 27 fathoms; Feb. 5, 1889 (46331; 46344). San Diego, Calif.; Albatross, 1897–8 (59545). Off Point Loma, San Diego, Calif.; in deep water; Nov. 7, 1889 (41905; the lectotype). Off the southern boundary of California; Albatross Station 2934; lat. 32°33′30″ N. long. 117°16′ W; 36 fathoms; Jan. 26, 1889 (46421). Off Bahia de Ballenas, Lower California: Albatross Station 3044; lat. 26°16′15″ N. long. 113°42′15″ W; 58 fathoms; Apr. 10, 1889 (46419); Albatross Station 3039; lat. 24°27′ N. long. 111°59′ W; 47 fathoms; April 8, 1889. Off Cape Tepoca, Gulf of California; Albatross Station 3018; lat. 30°16′ N. long. 113°05′ W; 36 fathoms; Mar. 24, 1889 (46342). Total number of specimens studied 16, 54 to 332 mm.

Geographic and vertical distribution.—The geographic range of the species as established by the material examined extends from off Santa Barbara, Calif., to near the northern end of the Gulf of California; the range in depth being 21 to 58 fathoms. The record by Starks and Morris carries the distribution northward to Point Conception, Calif. Gilbert (1915) records a depth of 74 fathoms.

Size.—The largest specimen examined 334 mm. (13 inches), 275 mm. without the caudal, stands for the present as the record size of the species.

Distinctive characters and relationship.—This species differs from *bollmani* chiefly in the number of gill rakers, the total number on the first gill arch being 15 to 21 in *stomata* and 11 to 13 in *bollmani;* although it is possible that when larger series are counted the two species may be found to approach one another in that character or even to intergrade. It usually has more numerous scales on the maxillary than *bollmani*, and these scales are ctenoid instead of being cycloid as in that species. Most specimens of medium size may be distinguished by the extent of the ctenoid scales usually extending forward to the posterior end of the arch in the lateral line in *stomata*, and usually nearly to the gill opening in *bollmani*, but sometimes individual fish cannot be distinguished on that basis. Other important differences are found in *stomata* having, on the average, more numerous dorsal and anal rays, a deeper body and longer maxillary than *bollmani*, but there is considerable intergradations in those characters, although the two species will no doubt prove to have distinct modes even after much greater numbers are studied. This species is evidently more closely related to *mystacium* than to *bollmani*, as far as shown by the structural characters. The relation of *stomata* to *mystacium* and to *macrops* is discussed under the accounts of the latter two species.

Hippoglossina stomata Eigenmann, Proc. California Acad. Sci. (2) 3: 22, 1893 (off San Diego, Calif.; in deep water).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3): 2620, 1898 (after Eigenmann).—Gilbert, Rept. U. S. Comm. Fish. 1898: 28, 1899 (off Catalina Island, Calif.; 47 fathoms).—Starks and Morris, Pub. Univ. California (Zool.) 3: 242, 1907 (off southern part of Lower California, north to Point Conception).—Metz, First Ann. Rept. Laguna Lab., p. 60, 1912 (Newport, Calif.; recorded under *Hippoglossoides*).—Gilbert, Proc. U. S. Nat. Mus. 48: 377, 1915 (Point Conception to Ballenas Bay; 21—74 fathoms).—Hubbs, Pub. Univ. Calif. (Zool.) 16: 168, 1916 (San Diego Market).—Starks, California Fish and Game 4: 168, fig. 87, 1918 (brief general account).—Ulrey and Greeley, Bull. Southern California Acad. Sci. 28 (1): 26, 1928 (Catalina I., Long Beach, Newport, Point Firmin, Venice, San Diego, all localities in California).—Norman, Monogr. Flatfishes, p. 66, fig. 34, 1934 (reviewed).

Hippoglossina bollmani Hiyama, Marine Fishes of the Pacific coast of Mexico, edited by T. Kumada, p. 59, pl. 92, fig. A, 1937 (Mexico, no definite locality given; the inadequate account agrees most nearly with *stomata* and is probably based on specimens of this species).

HIPPOGLOSSINA MACROPS

This species was described from Mazatlan, the Pacific Coast of Mexico, based on specimens "11–12 Zoll" long. The most essential characters as stated in the original description are as follows: Scales on eyed side of body all ctenoid, on blind side ctenoid scales present only on posterior third, about 52, A. 52, D. 66 to 67, P. 10–12. Dorsal origin over middle of eye. The figure shows a very large eye and narrow interorbital. Teeth small. Maxillary extending to a vertical slightly behind middle of eye. Depth 43 to 45; head 33 or a little shorter; maxillary 13. Steindachner's figure shows a dextral flounder, but some statements in the original description are evidently based on a sinistral fish.

No specimens are available for comparison and the relation of this species to the other three described above must remain somewhat doubtful for the present. An important character, namely, the number of gill rakers is omitted from the original description. It apparently differs from the other three species in that the ctenoid scales on the blind side do not extend as far forward, being present only on the posterior third of the body, and in having a deeper body. It further differs from *stomata* in having a shorter maxillary.

The taxonomic status of this species which is the genotype of *Hippoglossina* is uncertain. The use of the name *macrops* has an interesting history which has a bearing on the status of the species, and the different authors are discussed here in chronological order, omitting the four references cited in the synonymy which are based on Steindachner's orginal account. The original specimens were stated by Steindachner to have been taken at Mazatlan, but later authors ascribed it to the coast of Chile, apparently without comparing their specimens with the types.

Günther (1881) merely lists this species from Trinidad Channel without describing his specimens. They were later described by Norman as discussed below.

Abbott (Proc. Acad. Nat. Sci. Philadelphia, 1899, p. 475, 1900) records a specimen from Valparaiso Harbor, Chile, which he states "agrees with the description of *H. macrops* so exactly in every detail as to leave no doubt whatever of its identity." This author concludes that the locality, Mazatlan, given in the original description, is an error. Abbott's specimen is dextral, has 6+11 gill rakers and a well developed, antrorse, preanal spine.

Lönnberg (Ergeb., Hamburger Magalh., Sammelr., Fische, p. 14, 1907) records two specimens under *H. macrops* without describing them, one from Smyth Channel, Straits of Magellan, and one from Coronel, Chile. Later, Norman (1937, see below) cites Lönnberg's record, with a query, under two species, evidently suggesting that the two specimens mentioned possibly belong to one or two species, *mystacium* and *macrops*.

Norman (Monogr., p. 67, 1934) gives a description of two of Günther's specimens under the name of *H. macrops*. Later, Norman (Discovery Rept. vol. 16, p. 132, 1937) examined another specimen from the coast of Chile which proved to differ specifically from the two specimens he previously (1934) referred to *macrops*. Norman now concludes that the two specimens previously recorded by him and by Günther as *macrops* belong to *mystacium* while his later specimen, taken at lat. 38°22′, represents *macrops*. Its essential characters are as follows: Scales about 51; ctenoid scales on blind side only on posterior part of the body. Gill rakers 12 on lower limb. A. 56; D. 69. Pectoral of eyed side with 12 rays. Maxillary extending to below middle of eye. Head about 33; depth 42.

It is not possible to surmise what Abbott's and Lönnberg's specimens represent. They must be restudied and their pertinent characters established. As to Norman's specimen, it evidently is different from any of the three species examined by me; but whether it represents *macrops* is another question. The fish fauna of Mazatlan, the offshore fishes in particular, are not well enough known to be sure that a certain species does not occur there. Considering that *stomata* which seems to be closely related, has been taken on the Pacific Coast of Mexico, it is altogether within the realm of possibility that a species corresponding to the description of *macrops* will also be found to exist on that coast, and that two closely related species of the same genus live side by side. Should this surmise prove to be true, the probabilities are that none of the 4 specimens examined by the last-named three authors represent *macrops*, because nearly all of the species treated here have a comparatively restricted geographic distribution. Another possibility is that the original account of *macrops* is not quite accurate and that the species here described as *stomata* represents Steindachner's *macrops*. This suggestion is fortified by the fact that *stomata* is a common species and that it has apparently been taken on the Pacific coast of Mexico as recorded by Hiyama p. 291).

Hippoglossina macrops Steindachner, Sitzb. Ak. Wiss. Wien 74 (1) : 161 (Ichth Beit. 5: 13), pl. 3, 1876 (Mazatlan, Mexico).—Jordan and Goss Rept. U. S. Comm. Fish. 1886: 242, 1889 (after Steindachner).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3) : 2621, 1898 (after Steindachner).—Jordan and others, Rep. U. S. Comm. Fish. 1928: 223, 1930 (listed).

Subgenus Lioglossina

Lioglossina Gilbert, Proc. U. S. Nat. Mus. 13: 122, 1891 (genotype *Hippoglossina tetrophthalmus* (Gilbert) = *Lioglossina tetrophthalmus* Gilbert by original designation).

This subgenus differs structurally but slightly from *Hippoglossina*. The most striking difference is in the size of the eye which is notably large in the species of the subgenus *Hippoglossina* and not so large in the two species here placed in the subgenus *Lioglossina*. Combined with this difference is the somewhat more anterior position of the dorsal origin with respect to the anterior margin of the eye in medium-sized and large specimens of *Lioglossina*, and the weakly developed preanal spine which does not project exteriorly. Still another difference is found in the number of scales which is greater in the two known species of *Liogossina;* but since the number of available specimens in most species of these two subgenera is limited, the value of this character is uncertain. Quite probably, counts of more specimens will show a certain degree of intergradation. Other differences are given in the key. While these differences are hardly sufficient for subgeneric division, the species of *Hippoglossina* have a markedly distinctive physiognomy, due chiefly to their strikingly large eye and the 6 conspicuous spots. A consideration of all the characters makes it seem desirable to maintain *Lioglossina* as a subgenus distinct from *Hippoglossina*.

Lioglossina was originally based on, and distinguished from *Hippoglossina* by its cycloid scales. This seems adequate as far as the genotype, *tetrophthalmus*, is concerned. However, *oblonga*, which is obviously most nearly related to *tetrophthalmus* (p. 297), always has at least some ctenoid scales. Their number in that species is subject to great individual variability and some specimens have very few ctenoid scales (p. 294). It would seem to do violence to a natural arrangement of the species to place *oblonga* and *tetrophthalmus* in separate subgenera. The presence or absence of ctenoid scales in this subgenus is, therefore, regarded as of specific importance only, although in *Paralichthys* where this character clearly distinguishes two groups of related species, it is used for subgeneric division. The two known species are American.

HIPPOGLOSSINA OBLONGA
Fourspotted flounder
(PLATE 3)

Common name.—The four prominent spots on the eyed side of this species, usually surrounded by a ring of lighter color, suggests an appropriate common name for it, as given above. This name is generally employed in accounts of the species, and is here adopted. This common name conflicts with that of another species, *Ancyclopsetta quadrocellata*, which occurs in shallow water on the coast of the southern States. In order to distinguish the shallow water species, the name "fourspotted shoal flounder" is suggested for the latter fish, and since the present species is the more important one from an economic point of view, the shorter name is adopted for it.

Diagnosis.—At least a few ctenoid scales present on blind side of caudal peduncle in fish between 60 and 75 mm. or longer; ctenoid scales present on eyed side of head in large specimens, usually present also on posterior part of body on both sides; the number of spinuliferous scales highly variable; scales 63 to 81. No accessory scales. Gill rakers on lower limb of first arch rather short and stumpy, usually 8 or 9 in number, sometimes 7 or 10; on upper limb usually 2 gill rakers at angle somewhat similar to those of lower limb, and 3 to 5, usually 4, tuberosities above; tuberosities rarely becoming somewhat elongate, resembling short chunky gill rakers; sometimes the uppermost one of the two gill rakers at the angle shortened resembling the tuberosities; total number of gill rakers, not including the tuberosities, usually 10 or 11, sometimes 9, infrequently 12 or 13. (The structure and number of gill rakers, as described, is the same in the smallest specimens examined, 44 mm.; the tuberosities, therefore, not representing the stumps of gill rakers of young fish, but being the normal condition in this species, probably representing a remnant of a more remote phylogenetic condition.) Anal rays 58 to 72; dorsal rays 72 to 86. Pectoral rays usually 11, frequently 12, sometimes 10 (11 on both sides in 5 specimens, 12 on both sides in 3, 10 on blind side and 11 on the other in 1, 11 on blind side, and 12 on the other in 3). Origin of dorsal usually over anterior margin of pupil in small fish, generally over space between anterior margin of eye and that of pupil in medium-sized and large specimens. Teeth subequal in small fish,

a few anterior maxillary teeth becoming moderately enlarged in large individuals, more so than in other species of *Hippoglossina*. End of maxillary falling on a vertical through middle of eye at 50 mm., generally under posterior margin of pupil at 75 mm., under space between posterior margin of pupil and that of eye in large specimens. Interorbital a mere ridge; eye medium large; depth 39.5 to 43.5; head 25 to 29; maxillary 11.7 to 13.6; upper orbit 7.4 to 9.3; upper eyeball 6.1 to 7.6 (measurements of 11 specimens 244 to 328 mm.). Sinistral.

Development and variability of spinules on the scales.—The spinules begin to appear first on the scales of the blind side when the fish reaches a total length of about 60 mm., as a rule, sometimes not appearing until 70 or 75 mm. The scales at the base of the caudal are the first ones to develop spinules. In fish of that length the spinules are visible as well marked, tiny, and somewhat rounded points clearly and cleanly projecting beyond the margin of the scale. As the fish continues to grow the spinules appear successively on the more anterior scales. At the beginning a single conspicuous spinule appears on any one of the scales, the number of spinules increasing with size. During the process of development, therefore, the posterior scales, at the base of the caudal may have several conspicuous spinules, the anteriormost ctenoid scales, one spinule each, the numbers on each scale gradually decreasing from behind anteriorly. The spinules on the scales of the eyed side appear much later, sometimes in fish of about 100 to 110 mm., and quite often not appearing in fish as long as 135 mm. or longer. The spinules on any one scale of the blind side are generally more numerous and somewhat stronger than on the eyed side.

While the ctenoid scales increase gradually in number with size, their numbers are also highly variable with individual fish. In large fish they are nearly always present on the caudal peduncle of both sides, infrequently on the blind side only, and are also nearly always present on the eyed side of the head. Sometimes the spinuliferous scales extend over the posterior half or even two-thirds of the body, rarely over nearly the entire body. The spinuliferous scales are usually more numerous, and the spinules are somewhat better developed on the blind side, but sometimes they are more numerous on the eyed side. The spinules sometimes become visible only after drying the specimen, especially in those which are thickly covered with mucus, but they may always be felt by passing the sensitive tip of the finger forward over the surface of the fish.

Color.—Body always having 4 strongly marked ocellated spots in the same and characteristic positions; one each near the ends of the dorsal and anal fins, respectively; and one each near the dorsal and ventral profiles, on a vertical a little nearer to the head than the base of the caudal. Body and head otherwise variously mottled with lighter and darker shades. Ventral of eyed side with a small black spot at its distal margin; small specimens having this spot diffuse, or with three diffuse spots side by side. The caudal, dorsal, and anal on blind side characteristically peppered with minute dark chromatophores, distally.

The 4 characteristic ocellated spots are present in the smallest specimens examined, 40 mm. In small fish, 40 to 50 mm., the eyed side is thickly and uniformly spotted with small specks which may be more or less confluent, while the blind side is more or less profusely, but not thickly, sprinkled with minute clear cut dots which do not coalesce. The chromatophores on the blind side, except for the fins as described above, become more diffusely scattered at 60 mm. and entirely disappear at 75 mm.

Size.—This is a comparatively small species. The bulk of the specimens captured are about 12 inches or less. The maximum length on record is that given by Storer (1863), 16 inches. The largest examined is 13½ inches (340 mm.). Nichols and Breder (1927) record a maximum length of 15 inches, and a weight of 13 ounces.

Distinctive characters and relationship.—There is no trouble in properly identifying specimens belonging to this species. The characteristic position of the four prominent ocellated spots is unlike that of any other related American species found in the Atlantic. Also, the spots are unusually well marked, even in preserved specimens, as compared with the other related species. In rare cases, when the spots become faint in preserved fish, they may be identified by a combination of structural characters, namely, the absence of accessory scales, the presence of ctenoid scales, the comparatively small scales, and the few gill rakers. Its nearest relative

is evidently *P. tetrophthalmus* from the Pacific. The latter species besides agreeing with *oblonga* in nearly all the essential characters also has the same color pattern.

Specimens examined.—Provincetown, Mass. (24365). Cape Cod Bay, Mass. (24334; lat. 41°55′ long. 70°07′, 6 fathoms). Off Nantucket, Mass. (33359, lat. 40°43′ long. 70°45, 31 fathoms). Woods Hole, Mass. (10731; 45601). Vineyard Sound, Mass. (54905, 54910, 54916, 54927, 54933, and 54890). Menemsha Bight, Martha's Vineyard, Mass. (16552; 28702). Katama Bay, Martha's Vineyard, Mass. (58859). Buzzards Bay, Mass. (28861). West Bay, Newport, R. I. (25853, 12.5 fathoms; 25893, 5 fathoms). Noank, Conn. (14036). Long Island Sound at Milford (67600) and Stratford (67613; 676618; 67628), Conn. Long Island Sound, N. Y. (70207; 73413). Orient, Long Island, N. Y. (7061 A. M. N. H.). Tompkinsville, N. Y. (15089). Off Long Island (31673, lat. 40°03′ long. 70°45′, 70 fathoms; 31672, lat. 40°02′ long. 70°45′, 89 fathoms; 31691, lat. 40°02′ long. 70°35′, 100 fathoms; 33023, lat. 40°02′ long. 70°27′, 239 fathoms; 28711, lat. 40°01′ 24″ long. 70°46′, 98 fathoms). Off New Jersey (33534, lat. 39°59′ 15″ long. 70°36′30″, 143 fathoms; 28752, lat. 39°54′ long. 69°51′30″, 134 fathoms; 35508, lat. 39°33′40″ long. 72°08′45″, 87 fathoms; 33022, lat. 39°29′ long. 72°19′55″, 74 fathoms). Off Virginia (32684, lat. 37°19′45″ long. 74°26′06″, 102 fathoms). Off North Carolina (32785 lat. 36°38′30″ long. 74°40′10″, 81 fathoms; 45600, lat. 35°38′ long. 74°53′, 49 fathoms). Off South Carolina (45669, lat. 32°53′ long. 77°53′, 99 fathoms). About 15 miles south of Tortugas. Longley (92042). Total number of specimens examined 113, 40 to 340 mm.

Geographic and vertical distribution.—Northward this species has been recorded from Gloucester Harbor and also from Salem Harbor, Mass., by Goode and Bean (1879), as *Chaenopsetta oblonga* and as *Pseudorhombus oblongus*. However, later (1896) the same authors state: "The northern limits of its range is marked by the capture of a single small individual in 1877, off the mouth of Salem Harbor." This would make it seem likely that their previous reference to Gloucester Harbor was an error, but the authors may have overlooked that record. There is also a record from farther north on the register of the National Museum, apparently unpublished heretofore, namely, off Nova Scotia, lat. 45°25′ N. long. 57°10′ W., 170 fathoms. This record (23905) entered in the register in 1880 as *Pseudorhombus oblongus* could not be verified as to the identification, since the specimen is not available at present. The southernmost record previously published is apparently that of Longley (1941) from off Tortugas. The specimens examined as listed in the preceding paragraph cover the range from Provincetown, Mass., to Tortugas, Fla.

The vertical distribution of the species is interesting in that it varies from north to south. Near the northern end of its range, between Massachusetts and New York, it is common in comparatively shallow water just off the coast and in the larger bays and sounds where it is sometimes taken in large numbers between 5 and 15 fathoms. South of New York, however, it appears to be essentially a deeper-water species, occurring in water beyond the 20-fathom line. This evidently explains the paucity of records for this species south of New York, since so little trawling is carried on farther south in deep water. (At the northern extreme end of its range it possibly also occurs in deep water only, judging by the record from off Nova Scotia mentioned in the preceding paragraph.) The greatest depth at which it was taken is 239 fathoms (33023).

Biology.—No comprehensive study of this flounder was ever published and very little is known about the life history of the species. Smith (1898) states that: "The fish spawns in May and its eggs have been experimentally hatched at Woods Hole. The eggs are buoyant, one-twenty-sixth of an inch in diameter, and hatch in eight days in water having a mean temperature of 51° to 56° F." Bigelow and Schroeder (1936) record the capture of ripe specimens in mid-July. Some pelagic larvae taken by Bigelow and Welsh (1924) off the coast of New Jersey on July 19 and August 1, 1913, 8 to 11 mm. have been tentatively identified by those authors as belonging to this species. Fish of about 40 mm. are taken on the bottom with dredges or trawls.

The National Museum has a number of young fish for some of which the dates of capture are known. Since it is quite likely that no extensive study of this species will be undertaken for some time to come, it seems desirable to work up the

data which are presented in table 9. The data are too meager for general conclusions. However, they seem to indicate that the young reach a length of 80 to 160 mm. (3 to 6 inches) by the end of September. It seems also that the variation from year to year in the length at a given date is rather moderate.

Economic importance.—Although this fish is sold in the market, there is no way of gauging its importance in the flounder fishery, since those marketed are not sold under a distinctive name but are lumped with other flounders. Because of the small size, its economic importance is probably not great. It sometimes occurs in quantity from New York to Massachusetts beyond the five fathom line and is taken in dredges, trawls, or weirs. At Woods Hole, Mass., it is most common during May and June, while off New York it is "common in rather deep water" in November (Nichols and Breder). Pearson (1932) found it to a small extent in the winter trawl fishery off Virginia and North Carolina. This author, however, does not state whether the species was taken off the coast of both States, or only off the coast of Virginia. Judging by the vertical distribution of this species (p. 295), it seems probable that it does not occur in any numbers in the shallower waters off North Carolina where the winter trawlers operate. Farther south it is seldom captured apparently because the usual fishing operations do not extend to the depths inhabited by this species in southern waters.

Pleuronectes oblongus Mitchill, Trans. Litt. and Phil. Soc. New York 1: 391, 1815 (New York).

Platessa quadrocellata Storer, Proc. Boston Soc. Nat. Hist. 2: 242, 1848 (Provincetown, Mass.)

Platessa quadrocularis Gill, Cat. Fish. N. Amer. (supp. Proc. Acad. Nat. Sci., Philadelphia, 1861), p. 51, 1861 (no description, only a citation to Storer; change of name either a lapsus, or regarded more appropriate).

Platessa quadrocellata Storer, Mem. Amer. Acad. Arts Sci., Boston 8: 397, pl. 31, fig. 3, 1864; also in Hist. Fish. Mass., p. 203, 1867 (Provincetown, Mass.).

Chaenopsetta oblonga Gill, Proc. Acad. Nat. Sci., Philadelphia, 1864: 218 and 223.

Pseudorhombus oblongus Lyman, Sixth Ann. Rep. Comm. Inland Fish. Massachusetts, p. 47, 1872 (Waquoit, Mass.).

Chaenopsetta oblonga Baird, Rept. U. S. Comm. Fish. 1871–72, p. 824, 1873 (Woods Hole, Mass.).—Goode and Bean, Amer. Jour. Sci. Art. (3) 17: 40, 1879 (Gloucester Harbor).

Pseudorhombus oblongus Goode and Bean, Bull. Essex Inst. 11: 7, 1879 (mouth of Salem Harbor).—Bean, Proc. U. S. Nat. Mus. 3: 79, 1880 (Noank, Conn.; Woods Hole and Provincetown, Mass.).

Paralichthys oblongus Goode, Proc. U. S. Nat. Mus. 3: 472, 1881 (Station 873, off Martha's Vineyard, lat. 40°02′ N., long. 70°57′ W., 100 fath.).—Jordan and Gilbert, Bull. U. S. Nat. Mus. 16: 824, 1883 (specimens from Woods Hole, Mass.).—Bean, Rept. U. S. Comm. Fish., 1882: 340, 1884 (Woods Hole, Mass.).—Goode, Fish. Ind. U. S., Sec. 1, p. 181, pl. 43, 1884 (Salem Harbor, Mass.; New York to New England).—Jordan and Goss, Rept. U. S. Comm. Fish., 1886, p. 249, pl. 3, fig. 8, 1889.—Goode and Bean, Ocean. Ichth., p. 436, 1896 (mouth of Salem Harbor, Mass.; Buzzards Bay, Mass.; off Virginia, lat. 37°07′ N., long. 74°34′30″ W., 46 fath.; off N. Carolina, lat. 35°58′ N., long. 74°53′ W., 49 fath., lat. 35°42′ N., long. 74°54′30″ W., 43 fath.; off S. Carolina, lat. 32°53′ N., long. 77°53′ W., 99 fath.; general range given as Florida to Massachusetts).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3): 2632, pl. 374, fig. 924, 1898 (Woods Hole, Mass.).—Smith, Bull. U. S. Bur. Fish. 17: 108, 1898 (Woods Hole, Mass.).—Bumpus, Thirtieth Ann. Rept. Comm. Inland Fish. Rhode Island, p. 53, 1900 (Narragansett Bay, R. I.).—Bean, 6th Ann. Rept. Forest Fish Game Comm. New York [Cat. Fish. Long Island], p. 473, 1901.—Bean, 7th Rept. Forest Fish Game Comm. New York [Food and

Table 9.—*Length frequency distribution, by date of capture, of some young individuals of* Hippoglossina oblonga

Length	Aug. 16–23, 1880, Narragansett Bay, R. I.	Aug. 26, Buzzards Bay, Mass.	Aug. 29, 1879, Cape Cod Bay, Mass.	Sept. 3, 1875, Menemsha Bight, Mass.	Sept. 3–9, 1892, Vineyard Sound, Mass.	Sept. 10, 1874, Noank, Conn.	Sept. 17, 1890, Long Island Sound, N. Y.	Sept. 19, 1899, Katama Bay, Mass.	Sept. 25, Long Island Sound, N. Y.	Sept. 29, Long Island Sound, N. Y.	Sept. 29–30, 1892, Vineyard Sound, Mass.	Oct. 1–8, 1890, Long Island Sound, N. Y.
40 millimeters					1							
50 millimeters		3			1							
60 millimeters		2		2	2		1					
70 millimeters	1	1										
80 millimeters	2	3	2								1	
90 millimeters	2	3	2									
100 millimeters	2		5		3	1			1			1
110 millimeters			4		4					1	1	1
120 millimeters			1		3			1			1	1
130 millimeters	1		2									
140 millimeters												2
150 millimeters												
160 millimeters												1

Game Fishes of New York], p. 157, fig., 1902 (New York).—Bean, Cat. Fish. New York, p. 721, 1903.—Sharp and Fowler, Proc. Acad. Nat. Sci. Philadelphia 56: 512, 1904 (Nantucket, Mass.).—Kendall, Occ. Pap. Boston Soc. Nat. Hist. 7 (8): 147, 1908 (Gayhead, North Truro and Monomoy, Mass.; off Stratford, off Bridgeport, Middle Ground, off Faulkners Island, off South West Ledge and off Branford Beacon, Conn.).—Tracy, Fortieth Rept. Comm. Inland Fish. Rhode Island, p. 162, 1910 (R. I.).—Kendall, Rept. Comm. Fish. Game Massachusetts, 1910: 151, 1911 (Tisbury Great Pond, Mass.).—Sumner, Osburn, and Cole, Bull. U. S. Bur. Fish. 31 (1): 163, chart 208, 1913 (Woods Hole, Mass.).—Bigelow and Welsh, ibid. 40 (1): 494, fig. 205, 1925.—Nichols and Breder, Zoologica 9: 177, fig. 252, 1927 (Orient and Sandy Hook Bay, N. Y.).—Schroeder, Copeia, 1931: 45 (Off New Jersey, lat. 39°23′ N., long. 72°18′ W., 88 fathoms; lat. 40°04′ N., long. 73°14′ W., 28 fath. Off Rockaway, New York, 11 fath.).—Pearson, U. S. Comm. Fish., Inv. Rept. 1 (10): 24, 1932 (off Virginia and North Carolina, taken in the winter trawl fishery).—Norman, Monogr. Flatfishes, p. 79, fig. 45, 1934 (Woods Hole, Vineyard Sound, and Buzzards Bay, Mass.; off Long Island, N. Y.).

Hippoglossina oblonga Ginsburg, Jour. Washington Acad. Sci. 26: 131, 1936 (systematic position discussed).

Paralichthys oblongus Bigelow and Schroeder, Bull. U. S. Bur. Fish. 48 (20): 340, 1936 (southern half of Georges Bank; Virginia Capes; depth 10–112 fathoms).—Longley, Carnegie Inst. Washington Publ. 535: 39, 1941 (Tortugas, deep water).

HIPPOGLOSSINA TETROPHTHALMUS

(PLATE 4)

Diagnosis.—Scales all cycloid on both sides in small as well as large specimens; 63 to 69. No accessory scales. Gill rakers rather short, 2 on upper limb of first gill arch with 1 to 4 tubercles above, 9 to 10 on lower limb. Anal rays 58 to 63; dorsal rays 76 to 85. Pectoral rays 10 to 12 (10 on both sides in 1; 11 in another; 11 on eyed side, 10 on right in 1; 12 on eyed side, 11 on right in another). Origin of dorsal but slightly in front of anterior margin of pupil in large specimens, nearly over middle of eye in small fish. Teeth small and subequal, a few anterior ones in upper jaw but slightly enlarged. Maxillary reaching to a vertical through posterior margin of eye in large specimens, through posterior margin of pupil in small fish. Interorbital reduced to a mere ridge; eye large; depth 42 to 44.6; maxillary 13.9 to 14.1; head 29.5 to 30.1; upper orbit 8 to 9; upper eyeball 6.3 to 6.5 (measurements of 3 large specimens, 274 to 332 mm.; in 1 small specimen, 51 mm.; depth 38.8, maxillary 15.8, head 33.5, eyeball 10). Sinistral.

Color.—Four large, well-marked, ocellated spots on eyed side in approximately same position as in *oblonga*, but two foremost spots in a more posterior position, placed on a vertical about midway between hind margin of head and base of caudal. A large spot on ventral of eyed side at upper, distal angle, faintly ocellated in one specimen. Underside of vertical fins and caudal profusely sprinkled with minute dark dots, in one large specimen; blind side of body similarly sprinkled.

Lectotype.—Two specimens were described by Gilbert who did not designate a holotype, and U.S.N.M. 47290 is hereby designated as the lectotype.

Specimens examined and geographic distribution.—Gulf of California at Tiburon I., taken by the Albatross; 1 specimen 332 mm., Station 3014, lat. 28°28′ N., long. 112°04′30″ W., 29 fathoms, Mar. 23, 1889 (47290, the lectotype); 1 specimen 322 mm., Station 3016, lat. 29°40′ N., long. 112°57′ W., 76 fathoms, March 24, 1889 (47268). Gulf of California off Bahia de la Paz. Albatross Station 2822, lat. 24°16′ N., long. 110°22′ W., 21 fathoms, April 30, 1888, 1 specimen 51 mm. West coast of Lower California; Albatross Station 3038, lat. 24°24′30″ N., long. 111°53′ W., 31 fathoms, April 8, 1889; 1 specimen 274 mm. (47265). Total number of specimens studied 4, from localities ranging from off Tiburon I., at the northern end of the Gulf of California to off Magdalena Bay on the west coast of Lower California; the vertical distribution being 21 to 76 fathoms. Previous records apply to first two specimens, one from San Francisquito Bay not examined, and Hiyama's record of the west coast of Mexico without more definite locality.

Distinctive characters and relationship.—This species agrees with *oblonga* in all essential specific structural characters, except one. The origin of the dorsal is nearly the same in both species, and they have the same number of gill rakers, fin rays, and scales. The color pattern is also remarkably alike, there being but a slight difference in the position of the two anterior spots. This likeness appears to be a case of real affinity rather than parallelism. The only essential difference between the two species is that *tetrophthalmus* has all the scales cycloid while in *oblonga* some of the scales are ctenoid. However, in *oblonga* this character is highly variable, sometimes the greater number

of scales being ctenoid and in some individuals the ctenoid scales being very few. Indeed, if the four specimens of *tetrophthalmus* described above had been captured on the Atlantic coast, they readily might have been taken to be extreme variants of *oblonga* in which the ctenoid character of the scales was entirely lost, except for the difference in the position of the two anterior spots. The three large known specimens of *tetrophthalmus* have a somewhat deeper body and longer head and maxillary than average examples of *oblonga* of approximately the same size, but the latter species varies considerably in proportional measurements of the various parts, and when sufficient numbers are measured the two species very likely will be found to intergrade to a large extent in those respects. This species may readily be distinguished from all other related species on the Pacific coast of North and South America by its distinctive color pattern.

Lioglossina tetrophthalmus Gilbert, Proc. U. S. Nat. Mus. 13: 122, 1891 (Albatross Station 3014 and 3016; Gulf of California, off Tiburon I.).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3) : 2622, 1898.—Norman, Monogr Flatfishes, p. 69, fig. 37, 1934 (based on U.S.N.M. 47268 and 47290).—Breder, Bull. Bingham Ocean. Coll. 2 (3) : 3, 1936 (San Francisquito Bay, Gulf of California).—Hiyama, Marine Fishes of Pacific Coast of Mexico, edited by T. Kumada, p. 59, pl. 92, fig. B, 1937 (Mexico, definite locality not given).

PSEUDORHOMBUS

Pseudorhombus Bleeker, Versl. Med. Akad. Wet. Amsterdam 13: 436, 1862 (genotype *Pseudorhombus arsius* (Hamilton-Buchanan) = *Rhombus polyspilos* Bleeker by monotypy).

Pseudorhombus is intermediate between *Hippoglossina* and *Paralichthys*. It lacks accessory scales like *Hippoglossina* and has the dorsal origin over the anterior margin of the eye or a little more forward like nearly all species of *Paralichthys*. The interorbital width and the size of the eye and teeth differ with the species which form the intermediate links in a series showing a gradual transition from *Hippoglossina* to *Paralichthys* in these three characters. The color pattern is either somewhat like one or like the other of these two genera, or like a combination of the two, depending on the species. The prepeduncular spot is prominent in some species; the other prominent spots on the body are in two longitudinal rows in some species. The differences between *Pseudorhombus* and *Hippoglossina* are discussed on page 287. As compared with *Paralichthys*, the species comprised in *Pseudorhombus* are generally of smaller size and they have a somewhat different physiognomy. Their general appearance is probably what induced most later authors to maintain the species in a genus distinct from *Paralichthys*. As far as I could find after a review of the literature, two characters have been proposed, hitherto, for separating *Pseudorhombus* from *Paralichthys*, but neither one is tenable.

One of these characters was proposed by Jordan and Evermann (Proc. U. S. Nat. Mus. vol. 25, p. 365, 1902) who distinguished *Pseudorhombus* from *Paralichthys* by the former having an accessory branch of the lateral line and the latter lacking it. These authors were followed by Jordan and Starks (Proc. U. S. Nat. Mus. vol. 31, p. 173, 1906), by Weber (*Siboga* Exped., p. 414, 1913), by Norman (Monogr., p. 61, 1934), and probably by other authors who recognized *Pseudorhombus* as distinct. However, this character apparently does not hold. In the Indo-Pacific species now placed by authors in the genus *Pseudorhombus* the accessory branch is usually more clearly marked and better developed, extending to the dorsal profile, but in some of those species it apparently fails to reach there (see Norman, Monogr., figs. 59, 61, 63, and 65). The American species under consideration also have an anterior accessory branch of the lateral line more or less developed, although it generally does not extend to the dorsal profile. It is best developed in *californicus*, the genotype of *Paralichthys*, in which species it generally falls short of the dorsal profile, but in individual fish it often plainly extends to the dorsal fin, to the base of the fifth to the seventh ray. It is evident that as far as the accessory branch of the lateral line is concerned, the Indo-Pacific species do not differ generically from *californicus* and should be placed in *Paralichthys*.

The other character is that used by Regan (Ann. Mag. Nat. Hist., ser. 8, vol. 6, p. 492, 1910) who divides the two genera on the basis of the number of vertebrae, 10+24 in *Paralichthys* and 10+27 in *Pseudorhombus*. He does not state how many species nor the number of specimens examined to see whether this character is subject to individual variation intraspecifically, or to specific differences

within the genus. Two dissected specimens of *lethostigma* examined by me give counts of 11+27 and 10+27; of three specimens of *dentatus*, two have 11+30 and one has 11+31; one *squamilentus* has 10+28 and one *tropicus* has 10+26. Jordan and Goss (Rept. U. S. Comm. Fish. 1886, pp. 243–245, 1889) report the number of vertebrae as: *californicus* 10+25, *dentatus* 11+30, *albigutta* and *lethostigma* 10+27, *H. oblonga* 11+30. Thompson (Proc. U. S. Nat. Mus., vol. 50, p. 411, 1916) records the vertebrae of *brasiliensis* as 11+23. The number of vertebrae is, therefore, subject both to individual variation and to specific differences, and the numbers found in the American species which are universally accepted as being congeneric, cover the range of both *Pseudorhombus* and *Paralichthys* as given by Regan. Consequently, no two genera can be distinguished on that basis.

This leaves the absence of accessory scales as the best character by which *Pseudorhombus* may be distinguished from *Paralichthys*. This character is discussed on page 284.

PSEUDORHOMBUS ISOSCELES

(PLATE 5)

Diagnosis.—Scales etenoid on both sides, except those on cheek and opercle of blind side; 46 to 50 (counted on blind side in the three specimens examined, scales on eyed side largely fallen off); perforate scales 24 to 28 in arch and 50 to 51 in straight part to end of hypural. Accessory scales absent. Gill rakers on lower limb 8 or 9, comparatively short; upper limb with one gill raker at angle and 3 to 5 tuberosities above but slightly raised. Anal rays 66 to 68; dorsal rays 82 to 84. Pectoral 11, sometimes 10 (11 on both sides in two specimens, 10 on blind side, and 11 on the other in one specimen). Origin of dorsal in front of anterior margin of eye. Interorbital narrow, but wider than a mere ridge. Eyes rather large. Anterior teeth very moderately enlarged. Maxillary reaching posteriorly to a vertical through hind margin of eye or not quite that far. Depth 47 to 49.8, maxillary 13.9 to 14.3, head 26.9 to 29.3, upper eyeball 6 to 6.4, upper orbit 7.5 to 7.9, interorbital 1.3 to 1.6 (range of 3 specimens 243 to 260 mm.). Sinistral.

Color.—The color is nearly faded. Two large ocellated spots distinct, situated on a vertical almost midway between shoulder girdle and base of caudal, one at a short distance below the dorsal profile, and one at an equal distance from the ventral profile. A definite prepeduncular spot is not now present; but Jordan describes it in his original account, and a trace of such a spot is faintly perceptible. Ventral of eyed side with a small, oblong, rounded black spot at its distal margin.

Specimens examined and geographic distribution.—This account is based on three of Jordan's original specimens from Bahia, Brazil, 243–260 mm. (43335; 43368; 43371, herewith designated as the lectotype, 247 mm.). Norman's record (1937) extends the range of the species southward to latitude 45°05′.

Distinctive characters and relationship.—This species has etenoid scales on the blind side, unlike any species of *Paralichthys*. It also lacks accessory scales. In these two characters it agrees with the species of *Pseudorhombus*. No other, more substantial characters, are now known by which the two genera may be delimited, and if they are recognized as distinct at all, *isosceles* should be placed in *Pseudorhombus*. In their general appearance, regularity of arrangement and sharply defined edges, the scales of *isosceles* resemble those of *Pseudorhombus oligolepis* (Bleeker) with which it was compared. This species is readily distinguished from all closely related species of the western Atlantic, except *Hippoglossina oblonga*, by the presence of etenoid scales on both sides. It differs from *H. oblonga* in having fewer scales, in having nearly all scales etenoid and more strongly so, in the color pattern and in other characters given in the key.

This species, *H. oblonga* and *H. tetrophthalmus* have a black spot on the ventral of the eyed side. Attention is here called to this fact; because the possession of certain color marks in common, is often a good indicator of close relationship in fishes.

Paralichthys isosceles Jordan, Proc. U. S. Nat. Mus. 13: 330, 1890 (Bahia, Brazil).—Norman, Monogr. Flatfishes, p. 80, 1934 (based on original account).

Pseudorhombus isosceles Ginsburg, Jour. Washington Acad. Sci. 26: 131, 1936 (systematic position discussed).

Paralichthys isosceles Norman, Discovery Rept. 16: 134, 1937 (from four stations off the coast of Argentina between latitudes 43°50′ and 45°05′).

PARALICHTHYS

Definition.—Mouth symmetrical, large, maxillary reaching a vertical through middle of eye or more posteriorly, position of posterior extremity of maxillary depending largely on size of fish. Ventrals symmetrically placed on both sides of abdominal ridge, the fins from both sides subequal in length and in width of base. Pectoral longer on eyed side, base subequal on both sides, none of the rays notably prolonged. Body sinistral in most species, in 2 species varies with individual fish being nearly as often dextral as sinistral (another species is known from 1 dextral specimen). Lateral line present on both sides; with a well marked curve in front over pectoral fin; with an anterior accessory branch more or less developed, usually more or less disconnected from main lateral line, extending forward and more or less upward, generally not reaching dorsal profile, sometimes reaching there as an individual variation. (The accessory branch of the lateral line is somewhat better developed in *californicus*, *aestuarius*, *adspersus*, and *woolmani*, where it sometimes reaches the dorsal profile, especially in the larger specimens; but is present to a greater or lesser extent in all the species, is highly variable with the individual in its extent, and is evidently of no importance in distinguishing the species.) Teeth in jaws in one row, similar on both sides; the anterior teeth more or less enlarged, caninoid, especially those of upper jaw, but no marked fangs present; no teeth on vomer or palatines. Scales medium or small; ctenoid on eyed side and cycloid on blind side (in subgenus *Paralichthys;* some ctenoid scales infrequently present on caudal peduncle of blind side in *adspersus* and *californicus*, while in *aestuarius* the scales on eyed side become cycloid in large specimens); or scales all cycloid on both sides at all ages (in the subgenus *Chaenopsetta*). Accessory scales present, usually beginning to develop in fish reaching a length of 75 to 155 mm., the first appearance of accessory scales with respect to length differing with the species and to a lesser extent varying with individual fish. Gill membranes united, free from isthmus. Dorsal origin over or in front of anterior margin of upper eye in medium-sized or large specimens, more or less behind anterior margin of eye in young fish, nearly over middle of eye in adults, also, of one species; anterior dorsal rays not markedly prolonged. Rays of vertical fins simple, except hindmost; posterior 1 to 3 rays first becoming split in fish reaching a length of 40 to 60 mm., the number of branched rays and the number of dichotomous branchings increasing with size; total number of branched rays in large fish 5 to 15, with the posterior 2 or 3 sometimes branched dichotomously 3 times, except sometimes as an individual variation the ultimate ray and less often also the penultimate remaining simple in large specimens as well. The interorbital wider than a mere ridge, except in young fish; its width not differing notably with sex. Eye medium or rather small, the eyeball usually 5 percent of standard length or less in large or medium specimens. Gill rakers always considerably longer than wide, pointed or narrowly rounded at apex; few and more or less short and broad, to many and quite long and slender. Vertebrae 10 to 11+23 to 31, the number differing interspecifically, and somewhat varying intraspecifically with the individual (p. 299). Caudal rounded in young fish, becoming more or less biconcave in specimens over 100 or 200 mm., the biconcave condition becoming more pronounced with growth, the upper and lower angles becoming more or less produced in large fish. (The size at which the gradual changes occur and the relative development of the biconcave condition differs somewhat with the species but the differences are not sufficiently pronounced to be used in specific distinction.) Typical color pattern in 5 longitudinal rows of spots, the most prominent spots occupying various positions within the typical pattern depending on the species (p. 277). The prepeduncular spot prominent in most species, forming part of either the large or the small triangle or both.

Paralichthys is most nearly related to *Hippoglossina* and *Pseudorhombus* as discussed under those two genera (pp. 287 and 298). It is divisible into two subgenera, *Paralichthys* and *Chaenopsetta*. The following account of the genus includes all the known species except *olivaceus* from the coasts of Japan and China.

Subgenus Paralichthys

Paralichthys Girard, U. S. Pac. R. R. Explor. Surv. Zool., 10 (Fish.) p. 146, 1858 (genotype *Paralichthys californicus* (Ayres)=*Paralichthys maculosus* Girard by monotypy).

Uropsetta Gill., Proc. Acad. Nat. Sci., Philadelphia, 1862, p. 330 (genotype *Paralichthys californicus* (Ayres)= *Hippoglossus californicus* Ayres by monotypy).

Uropsetta Gill, ibid., 1864: pp. 194 and 198, (genus characterized for first time).

This subgenus differs from *Chaenopsetta* in having ctenoid scales on the eyed side. The scales become ctenoid when the fish is small, the smallest specimens examined already having the scales on the upper side spinulose (37 mm., total length of *aestuarius* and *adspersus* and 42 mm., *californicus*). In one species, *aestuarius*, the scales gradually lose their ctenoid character in fish between 160 and 220 mm., larger specimens having all scales cycloid with no trace of their former ctenoid condition. This gives a clue as to how the subgenus *Chaenopsetta* originated from species having ctenoid scales on the eyed side. Also, occasional specimens of *adspersus* and *californicus* have the caudal peduncle of the blind side more or less with spinuliferous scales, thus forming a transition to those species having ctenoid scales on both sides. All the species of the subgenus *Paralichthys* are American, with the exception of *olivaceus*.

PARALICHTHYS MICROPS

The following essential characters are compiled from Norman's two accounts of the species. Scales ctenoid on eyed side, cycloid on blind side; 54 to 65. Accessory scales present. Gill rakers 18–23 on lower limb. A. 56–65; D. 68–80. Pectoral about 2 in head, with 11–12 rays. Dorsal origin over middle or anterior half of eye. Eye 4.5–5.5 in head. (Norman's figure shows a rather narrow interorbital.) Canines moderate. Maxillary extending nearly to posterior edge of eye. Depth 43–50, head 29–32, maxillary about 14, sinistral. Mottled and spotted with darker, median fins blackish towards their margins.

Norman places *Paralichthys jordani* Steindachner in the synonymy of *microps*, with a query. Steindachner's species is based on three specimens, 217–280 mm. The pertinent characters given in the original description agree with those given by Norman for *microps* and outlined above, with the following exceptions: Scales about 62–70. Pectoral almost 1⅔ in head. Eye about 6 in head. Most scales finely margined posteriorly with dark brown, with a central brown point. Three longitudinal rows of grayish blue spots, along a median line and near dorsal and anal bases.

According to the original description *jordani* appears to have more numerous scales than *microps*, a character which usually indicates specific divergence in this group of fishes. The color of *jordani* also appears to be distinctively different. The apparent difference in the scale count may be due to different methods of counting or may fall within the range of variation of a single species. While the specimens on which the two names are based may possibly represent the same species, the probabilities are equally as good that they represent distinct species. This question may be determined only by a direct comparison of the types, or better still, by frequency distribution studies of numbers of specimens. Steindachner's specimens appear to have also a somewhat smaller eye and longer pectoral. Nevertheless, Steindachner does not satisfactorily prove that *jordani* is distinct. Pending further studies, Norman's treatment is here continued and the two names are associated under one heading.

This species is distinctively different from all other species of *Paralichthys* in the posterior position of the dorsal origin with reference to the anterior margin of the eye, agreeing with or approaching to the species of *Hippoglossina* in this respect. The dorsal origin in young fish is behind the anterior margin of the eye in all the species, but in *microps* this condition evidently persists in grown specimens also.

Hippoglossina microps Günther, Proc. Zool. Soc. London, 1881: 21 (west coast of Patagonia).—Jordon and Goss, Rept. U. S. Comm. Fish., 1886: 242, 1889 (after Günther).

Paralichthys jordani Steindachner, Faun. Chile 1: 325 [Zool. Jahrb. supp. bd. 4] 1898 (Puerto Montt, Robalo River, Chile).—Delfin, Cat. Pec. Chile, p. 104, 1901 (listed).

Hippoglossina microps Delfin, ibid., p. 103 (listed).

Paralichthys microps Norman, Monogr. Flatfishes, p. 88, fig. 52, 1934 (Chile; west coast of Patagonia).—Norman, Disc. Rept. 16: 133, 1937 (coast of Chile, near Conception and at latitude 38°22′).

PARALICHTHYS PATAGONICUS

Diagnosis.—Scales ctenoid on eyed side, cycloid on blind side; 76. Accessory scales present, moderately profuse. Gill rakers 2+10. Anal rays

66; dorsal 82. Pectoral with 12 rays, not quite but almost reaching to lateral line on eyed side, considerably short of lateral line on right side. Origin of dorsal slightly in front of anterior margin of eye. Maxillary reaching a vertical slightly past posterior margin of eye. Depth 43, head 26, maxillary 13, interorbital 2.3, eye 4.4, snout 6.9, left pectoral 13.1, right pectoral 10.7. Sinistral. The single specimen studied irregularly shaded, not showing any definite color pattern.

Specimen examined and geographic distribution.—The preceding account is based on a single specimen collected in Uruguay by Dr. Waldo L. Schmitt (87778). Records in the literature give a range for this species extending from Montevideo, Uruguay, to Bahia Blanca, Argentina. If the uncertain locality, Fort Famine, given by Günther for his specimen is correct, and the specimen in fact belongs to the present species, it would extend its range far to the south, to Magellan Strait. Also, if *Paralichthys bicyclophorus* Miranda Ribeiro is in fact a synonym, the range of the species would extend northward to the coast of Brazil.

Size.—The specimen examined, 410 mm. (16 inches), evidently must stand for the present as the record size to which the species attains.

Distinctive characters and relationships.—This is the only species of the typical subgenus which is now known from the Atlantic coast, and it may be separated from all other species of *Paralichthys* found in the Atlantic by its ctenoid scales on the eyed side. From *Pseudorhombus isosceles* which occurs in the same region with it, the present species is easily separable by the cycloid scales on the blind side and its smaller scales.

Synonymy and identification.—*P. bicyclophorus* is based on two specimens 330 mm. long from the Rio de Janeiro market. The pertinent specific characters given in the original account are: Scales ciliated (not stated whether only on one or on both sides); 68. Accessory scales present. Gill rakers 2 + 11; A. 65; D. 84. Maxillary nearly attaining to under posterior border of eye. Two prominent ocellated spots, one in the approximate position occupied by the prepeduncular spot in related species, the other and somewhat larger spot under the posterior bend in the lateral line.

In their original description of *patagonicus* Jordan and Goss state: ". . . dorsal rays 76; anal rays 60 . . . gill rakers 3 + 11". These counts and those given for *bicyclophorus* may fall within the range of variation of a single species, judging by all the species in which the frequency distribution has been determined. The authors of *patagonicus* fail to mention the structure of the scales, an important character in *Paralichthys*. William C. Schroeder kindly examined the three cotypes at my request and found the scales to be ctenoid on the eyed side and cycloid on the blind side, in 82 rows over the straight part of the lateral line which also agrees or nearly agrees with the types of *bicyclophorus*.

Mr. Schroeder describes in a letter the color of the types as follows: "Although faded, the 187 mm. specimen shows an ocellated spot about the size of the eye on lateral line, about four-fifths the distance from eye to hypural. The 160 mm. specimen shows the same and, in addition, several other obscure spots, one of them opposite the origin of the pectoral and below the lateral line where the arch joins the straight part. The 165 mm. specimen is too faded to show any spots." These notes when compared with the photograph published by Miranda Ribeiro of his *P. bicyclophorus* strongly suggest the possibility that the types of *patagonicus* originally had the same two prominent spots as Miranda Ribeiro's fish. The types of *patagonicus* and *bicyclophorus* are thus in apparent agreement in all the more important characters which differentiate the species of *Paralichthys* and the two names are most probably synonymous.

The specimen forming the basis of this account agrees almost perfectly with the types of *bicyclophorus* in its structural characters and it apparently also belongs to the same species. However, there is a discordant note with respect to the color. This specimen does not have the two prominent spots present in the types of *bicyclophorus* and apparently also in those of *patagonicus*. This specimen is larger than the five types discussed above and it is possible that, as in other species of *Paralichthys*, the prominent spots disappear with age. On the other hand, there is the possibility that the types of *patagonicus*, those of *bicyclophorus* and the specimen examined represent more than one species. A definite solution of this question must wait until more abundant material is examined.

Nomenclature.—In naming this species Jordan and Goss (1889) were anticipated by Jenyns (1842) who describes a specimen that evidently belongs to the same species under the name of *Platessa orbignyana;* as shown by his statement which agrees with this species, as follows: "Upper or eye side of the body slightly rough, with the scales finely ciliated; under-side smooth, the scales on this side not ciliated." Norman (1937) re-examined Jenyns' specimen, found it to have 10 gill rakers on the lower limb, and he states that it "should most probably be placed here [under *patagonicus*]." The question now is, what is the status of the name *orbignyana?* Most authors following Jenyns and Valenciennes, who used the name *orbignyana*, either as a valid name or in synonymy, possibly employed it not in accordance with the international rules.

The generally accepted dates of publication of Jenyns' work (Zool. Voy. Beagle), and D'Orbigny's work (Voy. Amer. Mérid.) where Valenciennes describes his *orbignyana*, are those given on the title pages, namely, 1842 and 1847, respectively. However, Jenyns in his supposedly earlier work refers in several places to the atlas of D'Orbigny's work. Under his account of *Platessa orbignyana* which he ascribes to Valenciennes, with a query, and cites the plate of that author, Jenyns states: "This species agrees so well with the figure of the *P. Orbignyana* in D'Orbigny's Voyage, that I have little hesitation in considering it the same,—but as no description of this last has been yet published, it is still possible I may be mistaken." An explanation of this discrepancy is offered by Norman (Monogr., p. 71, 1934) who states: "The fact that Jenyns quotes Valenciennes' name in 1842 appears to be due to the earlier publication of the Atlas of D'Orbigny's voyage." Norman's interpretation is reasonable. However, there may be yet another explanation. Jenyns might have examined the originals or the proofs of the plates before they were formally issued in such manner as to reasonably constitute "publication" that may be used in determining priority. In that case, the name *orbignyana* as used by Jenyns is a manuscript name, and according to Opinion 4 of the International Commission must be dated from that author's work and applied to that species represented by the specimen described by him, regardless of the fact that he cites it with a query, thus: "Platessa Orbignyana. Val. ?"

It is of course well known that the date on the title-page of a work often does not represent the true date of its issue. But in practice we must assume the published date is correct, unless unmistakable proof to the contrary is adduced. Otherwise, any stability in nomenclature will be impossible to attain, in some cases. It may require considerable research to determine the correct date of publication of some works, and in some others, older works especially, a most extended search may prove to be a labor in vain.

The status of *Platessa orbignyana* of Valenciennes cannot be determined now. The entire description consists of a single sentence, as follows: "Nouvelle espèce de limande caractérisée par la force des dents antérieures." This is of course inadequate to determine the species. At the most, it shows that he probably had a species of *Paralichthys*. The figure shows that it was drawn from a specimen representing a species of *Paralichthys*, but it is not sufficient for a definite, specific identification. It shows 74 dorsal rays, 55 anal rays, and 73 oblique rows of scales over the lateral line. The dorsal and scale counts agree with the two species here designated as *patagonicus* and *brasiliensis*, and the anal count more nearly agrees with the latter; but this does not offer satisfactory evidence regarding the disposal of Valenciennes' name. Mr. Paul Chabanaud kindly replied to my inquiry regarding the type, stating that it cannot be located.

On the assumption that Jenyns' use of that name has priority, it is not of much importance to determine Valenciennes' later use of the same name, except with respect to the proper placement of the synonymy. But, should it be definitely proved that, as suggested by Norman, Valenciennes' use of the name *orbignyana* has priority, its proper disposition becomes a matter of importance. It may be taken to be what it practically is: representing an unidentifiable species. It may also be suggested that later revisers be followed; but there may be differences of opinion as to which one of the later revisers to follow.

Assuming that Valenciennes' plate was published earlier, Jenyns (1842) is the first reviser; but he cites Valenciennes' name with a query, and

there may be some question whether his restriction is to be accepted. The next reviser is Günther (1860) who places both Valenciennes' and Jenyns' references under his account of *Pseudorhombus dentatus* with a query (possibly his account is based primarily on a specimen of the present species, but Norman, 1937, is not certain regarding its placement). Since Günther doubtfully cites his synonymy, it may also be questioned whether his action constitutes a definite restriction of the name *orbignyana*. On the other hand, he associates both Valenciennes' and Jenyns' references under one heading, and he may be said to have restricted both accounts to one species. Since Jenyns' description includes statements pertinent to its identification and his specimen is still in existence enabling a definite determination of its status, this is probably the best disposition that may be made of Valenciennes' name *orbignyana*. That is, accept Günther's restrictions of both accounts to the same species, and restrict the name *orbignyana* to that species represented by Jenyns' specimen, the status of which is now determinable.

Still later revisers are as follows: Jordan and Goss, 1889 place *orbignyana* in the synonymy of *brasiliensis*, and the same course is followed by Jordan and Evermann, 1898. Norman (1934) applies the name *orbignyana* to that species here designated as *brasiliensis* and switches the name *brasiliensis* to another species. The conflicting use of that name by these authors is apparently not in consonance with all the facts in the case or with the most reasonable usage indicated on a consideration of the various points involved.

On the basis of the evidence now available Jenyns' use of that name should evidently have preference, his specimen becomes the type of this species, and the name *orbignyana* is to be properly applied to it. Even assuming that *orbignyana* of Valenciennes has priority, its apparent best disposition is also to apply it to this species. Nevertheless, I continue the use of the name *patagonicus* for the following reasons: (1) It is not altogether certain which one of the later revisers is to be followed in disposing of Valenciennes' *orbignyana*. (2) The status of the material here grouped under this name is not entirely certain as discussed above, and it seems best to postpone this change of name, which must be confusing at first, until the status of the species is thoroughly cleared. (3) The name *patagonicus* was more frequently used for this species than any other name. Also, that name apparently was used for no other species and its continued use for this species will not lead to confusion. (4) The name *orbignyana*, either as a valid name or as a synonym, was generally applied by authors to other species than the present one and its substitution for this species would lead to further confusion.

Platessa orbignyana JENYNS, Zool. Voy. Beagle 4: 137, 1842 (Bahia Blanca).—VALENCIENNES, Voy. Amer. Merid. D'Orbigny 5 (2, poiss.) : 10, pl. 16, fig. 1, 1847 (Brazil).

Pseudorhombus dentatus GÜNTHER (not Linnaeus), Cat. Fish. British Mus. 4: 425, 1862 ("Probably brought by Capt. King from Port Famine"; specimen possibly belonging to this species; accounts of preceding two authors cited).

Paralichthys patagonicus JORDAN and Goss, Rept. U. S. Comm. Fish. 1886: 245 and 248, 1889 (east coast of Patagonia, types in Museum of Comparative Zoology).—Berg, An. Mus. Nac. Buenos Aires 4: 77, 1895 (Bahia Blanca and Mar del Plata, Argentina; Montevideo, Urnguay).—EVERMANN and KENDALL, Proc. U. S. Nat. Mus. 31: 107, 1906 (Buenos Aires market).

Paralichthys bicyclophorus MIRANDA RIBEIRO, Arch. Mus. Nac. Rio de Janeiro 17 (Heterosomata) : 14, photo., 1915 (Rio de Janeiro market).

Paralichthys patagonicus DEVINCENZI, An. Mus. Nac. Montevideo (2) 5: 278, 1924 (Urugnay).—MARINI, Rev. Soc. Argentina Cienc. Nat. 9: 454, 1929 (Puerto Quequen, Argentina).

Paralichthys brasiliensis NORMAN (in part), Monogr. Flatfishes, p. 77, fig. 44, 1934 (outline figure of type specimen of *patagonicus* published).

Paralichthys bicyclophorus NORMAN, ibid., p. 78 (after original account).—MCDONAGH, Rev. Mus. La Plata 34: 56, 1934 (Mar del Plata, Argentina).

Paralichthys patagonicus GINSBURG, Jour., Washington Acad. Sci. 26: 132, 1936 (stated to represent a distinct species and that *bicyclophorus* is probably the same).—NORMAN, Disc. Rept., 16: 133, 1937 (Buenos Aires).

PARALICHTHYS HILGENDORFII

This species is based on a single, malformed specimen, 273 mm., from Juan Fernandez, Chile. The original description gives the following pertinent specific characters. Scales ctenoid on eyed side, cycloid on blind side; about 62. Gill rakers 9 on lower limb of first gill arch; 6 on upper limb, the 4 anterior ones rudimentary. A. 61; D. 75; pectoral 2 in head with 11 rays. Dorsal origin over anterior margin of eye. Maxillary somewhat less than 2¼ in head; reaching to under posterior margin of orbit. Dextral. Eyed side grayish brown with a fine dark sprinkling.

This species apparently differs from both *schmitti* and *fernandezianus* in not having the blind side of the dorsal spotted and in having a shorter pectoral as compared with the head length. The single specimen known is apparently dextral while the other two species are sinistral. It further differs from *fernandezianus* in having fewer scales and possibly also fewer gill rakers, and from *schmitti* possibly in having fewer pectoral rays and a shorter maxillary.

Paralichthys hilgendorfii STEINDACHNER, Faun. Chilen. 3: 209 (Zool. Jahrb., supp., bd. 6) 1905 (Juan Fernandez, Chile).—NORMAN, Monogr. Flatfishes, p. 81, 1934 (after Steindachner).

PARALICHTHYS SCHMITTI

(PLATES 6 AND 7)

Diagnosis.—Scales ctenoid on eyed side, cycloid on blind side; 68. Accessory scales present on both sides, very numerous, nearly covering surface of many regular scales and massed in bands around edges of nearly all scales. Gill rakers short, 9 on lower limb of first gill arch, 3 on upper limb with 1 tubercle above. Anal rays 63; dorsal 80; pectoral 12. Origin of dorsal a little in advance of anterior margin of eye; maxillary extending posteriorly to a point a little behind a vertical through posterior margin of lower eye, 15. Body of medium depth, 44; head 30; interorbital rather wide, 3.2; pectoral 2.4 in head. Sinistral.

Color.—Blind side of head and body light-colored, like the normal condition in the species of *Paralichthys*, but unlike nearly all other species; the fins of underside, including the dorsal, anal, caudal and ventral, distinctly blotched. A narrow area along upper and lower margins of blind side, in front, speckled with small brown spots, the speckling continued, but less distinct on opposite side. Eyed side dark, irregularly shaded. Some diffuse spots of more or less greater intensity than the ground color; two or three faintly suggesting ocelli; no spots especially prominent. Pectoral and ventral of eyed side with irregular transverse rows of somewhat elongate spots. Two diffuse curved bands on caudal, against an irregularly shaded background.

Specimen examined.—This species is known from the single type specimen, 455 mm. (88831), taken at Juan Fernandez Island, off the coast of Chile.

Distinctive characters and relationship.—This species is apparently related to *fernandezianus* which also has the dorsal blotched on the blind side, an unusual color mark in a species of *Paralichthys;* but it differs in the less numerous scales. Although no material is available for comparison, it is to be noted that Steindachner who described *fernandezianus* also is the author of three other species of the subgenus *Paralichthys*, namely, *adspersus*, *jordani*, and *hilgendorfii* for which he gives the number of scales in the lateral line as 104, 92 to 105 and 94, respectively. These numbers closely agree with those found in the species of the subgenus *Paralichthys* studied by me (compare with table 6, taking into account the conversion factor given on p. 271). The scale count of *schmitti* also closely agrees with the majority of the species of its subgenus. On the other hand, the count of *fernandezianus* is given as, "L. l. c. 140." This is a number much greater than that found in *schmitti* as well as the three species described by Steindachner. From all the other American species of *Paralichthys*, except *fernandezianus*, *schmitti* may be distinguished by the fins being blotched on the blind side, and the other characters given in the key.

Paralichthys schmitti GINSBURG, Proc. U. S. Nat. Mus. 82 (20): 1, 1933 (Juan Fernandez Island, Chile).

PARALICHTHYS FERNANDEZIANUS

This species is based on a single specimen, 510 mm., from Juan Fernandez, Chile. The following important specific characters are taken from the original description: Scales ctenoid on eyed side cycloid on blind side; about 94. Accessory scales present. Gill rakers 3 on upper limb of first gill arch with 2 rudiments, 11 on lower limb. A. 60. D. 78. Pectoral slightly more than 2⅓ in head; with 11 rays. Origin of dorsal slightly in front of anterior margin of eye. Maxillary attaining past posterior margin of eye by a distance nearly equal to length of eye; 2⅓ in head. Sinistral. Dorsal on blind side marbled with irregular brown spots; eyed side with a fine dark sprinkling.

This species has the dorsal spotted on the blind side like *schmitti* differing in having more numerous scales, and possibly in having more gill rakers and the maxillary extending more backward with relation to the posterior margin of the eye.

Paralichthys fernandezianus STEINDACHNER, Faun. Chilen. 3: 208 (Zool. Jahrb. supp., bd. 6), 1905 (Juan Fernandez, Chile).—NORMAN, Monogr. Flatfishes, p. 87, 1934 (after Steindachner).

PARALICHTHYS ADSPERSUS

(PLATE 8)

Diagnosis.—Scales ctenoid on eyed side, typically cycloid on blind side (sometimes ctenoid scales present on caudal peduncle and adjacent hind part of body); 63 to 81. Accessory scales present; first occurring in specimens of about 100 mm.; appearance with respect to size varying individually, becoming very numerous with increase in size. Total number of gill rakers on outer arch 22 to 27, the majority having 25 or 26; 7 or 8 on upper limb, mostly 7; 15 to 19 on lower limb. Anal rays 54 to 61, 57 or 58 in the majority of individuals; dorsal rays 68 to 76. Pectoral rays usually 12 or 13, sometimes 11 (12 on both sides in 5 specimens, 13 in 3, 11 in 1, 12 on blind side and 13 on eyed side in 2, 13 on blind side and 12 on the other in 1, 11 on blind side and 12 on the other in 1). Origin of dorsal over space between anterior margin of eye and that of pupil in specimens 70 to 118 mm., over anterior margin of eye or nearly there in specimens 205 to 388 mm. Maxillary about reaching to a vertical through posterior margin of pupil in specimens 72 to 118 mm., to posterior margin of lower eye or slightly past that in specimens 205 to 388 mm. Head comparatively long. Body rather deep. Caudal usually becoming more or less biconcave in larger specimens, sometimes nearly rounded in large fish also. Sinistral.

Color.—Rows of spots more or less irregular, appearing like seven longitudinal rows in some specimens; many of the spots more or less ocellated; the three spots forming the larger triangle usually rather more prominent than the other spots. The ocellated spots are present in the largest specimen examined, 388 mm. Some of the spots frequently are more or less characteristically ring-like, the center being to some extent pigmentless or but sparsely pigmented. Underside of fins sprinkled with tiny dark dots, somewhat as in *H. oblonga* but not so profuse. White spots frequently present at bases of dorsal and anal fins, but not so well marked as in *californicus*.

Specimens examined.—Callao, Peru; P. O. Simmons, 2 specimens, 205–388 mm. (53490); R. E. Coker, 3 specimens, 239–276 mm. (77713 and 77715); R. C. Murphy, Callao market, 1 specimen 284 mm. (7273 A. M. N. H.). Chincha I., Peru. R. C. Murphy, 3 specimens 37–45 mm. (7911 A. M. N. H.); R. C. Murphy, Oct. 26, 1919, 1 specimen 275 mm. (7290 A. M. N. H.). Mollendo, Peru, R E. Coker, 1 specimen 245 mm. (77716). Tome, Chile, *Albatross*, 3 specimens 72–86 mm. (77390). Lota, Chile, Feb. 15, 1888, *Albatross*, 6 specimens 90–118 mm. (77391). Total number of specimens studied 20, 37 to 388 mm., in length.

Geographic distribution.—The material examined covers the range from Callao, Peru, to Lota, Chile; existing records also include this range and San Juan I. Extant records of "*Paralichthys adspersus*" from the Pacific coast of Mexico and Panama apparently are based on specimens of *Paralichthys woolmani* (p. 313).

Size.—The largest specimen examined, from Callao, Peru, is 388 mm. (15 inches) long, including the caudal fin. However, this may not represent the maximum for the species since those examined are museum specimens, and collectors usually select the smaller examples for preservation.

Distinctive characters and relationship.—Of the other species of the subgenus *Paralichthys* occurring on the coast of South America, *adspersus* may be distinguished from *fernandezianus*, *hilgendorfii* and *schmitti* by its more numerous gill rakers. From *microps* it differs in the more anterior insertion of the dorsal. This species is very near to *californicus* differing from the latter chiefly in having a deeper body, there being no intergrades between the two species in this character (table 8). The gill rakers in *adspersus* are less on the average than in *californicus*, and the fin rays are more numerous; but there is considerable intergradation in those characters (tables 1 to 5). *P. adspersus* is always sinistral, while *californicus* is often also dextral. This species intergrades with *aestuarius* in every character studied, except the structure of the scales in the larger specimens. Individual fish of these two species are separable only when they reach a size of about 200 mm., such specimens having the scales on the eyed side ctenoid in *adspersus* and all or almost all cycloid in *aestuarius* (p. 310).

Economic importance.—This is evidently a food fish on the coast of South America, and some of the

specimens studied have been obtained in the market at Callao, Peru; but there does not seem to be any data extant as to its abundance or the quantities marketed.

Pseudorhombus adspersus Steindachner, Sitzb. Akad. Wiss. Wien 55 (1): 709, pl. 2 (Ichthyol. Notiz. 5: 9) 1867 (Chincha Islands, Peru).

Paralichthys adspersus Jordan and Goss (in part), Rept. U. S. Comm. Fish. 1886: 246, 1889 (Callao).—Jordan (in part), Proc. California Acad. Sci. (2) 5: 503, 1895 (Callao, Peru).—Jordan and Evermann (in part), Bull. U. S. Nat. Mus. 47 (3): 2627 and 2872, 1898 (Callao, Peru).—Abbott, Proc. Acad. Nat. Sci., Philadelphia, 1899: 363, 1900 (Coast of Peru).—Steindachner, Fauna Chilensis 3: 208 (Zool. Jahrb. supp. bd. 6) 1905 (Juan Fernandez, Chile; specific name spelled *adspasus*).—Starks, Proc. U. S. Nat. Mus. 30: 809, 1906 (Callao, Peru).—Thompson, Proc. U. S. Nat. Mus. 50: 411 and 468, 1916 (Tome and Lota, Chile; Callao, Peru).—Evermann and Radcliffe, Bull. U. S. Nat. Mus. 95: 140, 1917 (Callao and Mollendo, Peru).—Nichols and Murphy, Bull. Amer. Mus. Nat. Hist. 46: 512, 1922 (Chincha Is., Peru).—Norman, Monogr. Flatfishes, p. 83, fig. 49, 1934 (Peru): Iquique, Lota, Pescadores Bay, and Juan Fernandez Island, Chile).

PARALICHTHYS CALIFORNICUS

California halibut

(PLATE 9)

Common names.—This species is commonly called halibut in California, a name which properly belongs to a distinct and quite different species of flatfish. It is also known as bastard halibut, Monterey halibut, chicken halibut, southern halibut, and alabato. "California halibut" has been adopted as a uniform common name for this species by the Division of Fish and Game of California.

Diagnosis.—Scales on eyed side ctenoid in large as well as in small fish, cycloid on blind side (the ctenoid scales sometimes extending in narrow bands at the dorsal and ventral edges of the caudal peduncle of the blind side; infrequently the spinuliferous scales spread over the entire surface of the caudal peduncle and the base of the caudal fin on the blind side); 62 to 78. Accessory scales present, first appearing on eyed side of head in specimens of about 100 mm., at about 135 mm. on eyed side of body and a little later on blind side; first appearance of accessory scales with respect to length varying with individual fish, becoming very numerous and nearly covering entire surface of normal scales with increasing size. Total number of gill rakes on outer arch 25 to 32, the majority having 28 or 29; usually 8 or 9 on upper limb, frequently 7, sometimes 10 or 11; lower limb with 18 to 23 gill rakers. Anal rays 49 to 59; dorsal rays 66 to 76. Pectoral rays usually 12, frequently 11 or 13 (12 on both sides in 15 specimens; 11 in 3; 13 in 2; 11 on blind side and 12 on eyed side in 4; 12 on blind side and 11 on other in 1; 12 on blind side and 13 on the other in 3). Origin of dorsal over anterior margin of pupil in specimens 50 to 85 mm., over space between anterior margin of eye and that of pupil in specimens 90 to 175 mm., generally over anterior margin of eye in specimens 175 to 300 mm., distinctly in front of eye in 1 specimen 473 mm., considerably in front in 1 specimen 570 mm. Posterior extremity of maxillary usually falling on a vertical through middle of eye or posterior margin of pupil in specimens 55 to 85 mm., through posterior margin of pupil to that of eye in fish up to about 150 mm., usually to posterior margin of eye in specimens 150 to 200 mm. and somewhat beyond eye in larger fish. Body rather slender or of medium depth; head and maxillary rather short. Often dextral. (Out of 123 fish examined, 77 were sinistral and 46 were dextral. It is to be noted that in lots of specimens of approximately the same size taken on the same date at the same locality, evidently from the same school having the same origin, the fish are preponderately either sinistral or dextral, suggesting that this character is of an hereditary nature).

Color.—Ocellated spots present in some of the small specimens examined, most of the others evidently faded from long immersion in preservative, and the frequency of occurrence of ocellated spots in fresh specimens is problematical. The rows of other spots, where present, are often more or less irregular. In those specimens in which the ocellated spots are present the three spots forming the larger triangle are often more prominent than the others, and sometimes present in specimens having no other ocellated spots than those three. A longitudinal, somewhat curved, row of six, white, small spots under and along the dorsal profile, beginning at a point over the preopercle and ending near the end of the dorsal; and a similar but usually less well-marked row over the base of the anal. These spots are frequently persistent in

preserved specimens which have otherwise nearly all faded. Sometimes numerous similar, white, small spots are scattered over the head and body, and in such specimens the longitudinal rows as described above are not as saliently marked, but even then the spots in the longitudinal rows stand out more prominently than the others. Most other species have white spots more or less developed, but they are usually most prominent in *californicus* and also in *aestuarius*.

Specimens examined.—San Diego, California (22 lots in Nat. Mus., 1 to 11 specimens in a lot, and one lot of 25 specimens, 18 of which are included in the tables). The following localities on the west coast of Lower California: San Quentin Bay (46561); San Bartolome Bay (47269: 59464); Puerto San Bartolome (A. M. N. H. 5460 and 5462); Ballenas Bay (A. M. N. H. 5452); Magdalena Bay (47286). Total number of specimens studied 123, 42 to 570 mm.; 15 from the west coast of Lower California; all others from San Diego.

Geographic distribution.—The specimens examined represent a range from San Diego Bay, Calif., to Magdalena Bay, Lower California. It has previously been reported from Tomales Bay, Calif., to Magdalena Bay, these two localities being the extremes of its range known at present. Its center of abundance is at San Diego; it is abundant at Monterey; at San Francisco it is not abundant although taken in moderate commercial quantities.

Size.—This is the largest species of *Paralichthys* in American waters. The largest fish of which there is any definite record is that reported by Lockington (1879), a specimen weighing 58 pounds, 4 feet 10 inches in length. The same author (1878–79) states that he was told that the fish reaches a weight of 70 pounds. Jordan and Gilbert (1881) record a fish of 55 pounds.

Distinctive characters and relationship.—This species is closely related to *aestuarius* and *adspersus*. From the latter it differs chiefly in the depth of body, there being no intergrading individuals in the many specimens examined although the extremes of the two species approach closely. The form of the frequency-distribution polygon for the number of gill rakers is different in the two species, but in this case there is considerable overlapping. *P. californicus* is most closely related to *aestuarius*, differing from the latter in that the scales retain their ctenoid character with age and in the smaller number of dorsal and anal rays, there being some intergrading in the latter characters. In practice, *californicus* may be readily distinguished from *adspersus* in its more slender body and also in their widely separated geographical ranges. From *aestuarius*, large specimens, those over 200 mm., may be distinguished by the character of the scales. Small specimens, however, may be distinguished only by the number of fin rays, and this is not reliable in every case (tables 5 and 6). Difficulty will, therefore, be experienced in identifying some isolated small specimens in the localities where the two species occur together. In fact this may prove impossible in the case of some individual small fish. If a fish has less than 74 dorsal and less than 56 anal rays, it is nearly always a *californicus*. The probability of its being an *aestuarius* is remote. Likewise, if a specimen has more than 77 dorsal and more than 60 anal rays it is most likely an *aestuarius;* the chance of its being *a californicus* is almost negligible. However, the identification of small specimens having 74 to 77 dorsal rays and 56 to 60 anal rays must be doubtful.

Biology.—Although it is a common and important species very little is known regarding its life history. Clark (1931) states that "spawning . . . occurs from February to July with its greatest intensity in May." According to this author, the fishermen think that when the fish become abundant in late winter or early spring they are migrating from greater depths to spawn nearer the coast. This would indicate a spawning migration in the opposite direction from that taken by the summer flounder on the east coast (p. 319). As to the rate of growth, Clark estimates a length of 1–5 inches for fish one year old; 4–9 inches at 2 years; 6–15 inches at 3 years; 10–16 inches at 4 years, and 11–17 inches at 5 years.

Fishery and economic importance.—The California halibut is one of the important food fishes on the coast of California and Lower California. The trammel net is an important gear by which this species is taken and is practically the only gear used around San Pedro due to legal restrictions (Clark 1931). The inner layer of the trammel nets used there has a mesh of 8 inches,

stretched. In other sections of the coast, it is also taken with trawl nets and with hook and line. The commercial catch is mostly obtained in water from 3 to 20 fathoms in depth. The California halibut is taken in commercial quantities the year-round, but the bulk of the catch on the American coast is taken between January and June, with the peak usually occurring during March. Of the total quantity obtained in Mexican waters and landed at American ports, the bulk is obtained between June and November with the peak of the catch during August (Whitehead 1929).[6]

The annual catch of the California halibut fluctuates from year to year, as does that of many other fishes. Superimposed on this annual fluctuation, a decline occurred in the commercial catch from more than 4 million pounds in 1916 to 1,787,901 pounds in 1947 (Calif. Bur. Mar. Fish., Bull. 74, p. 226, 1949). The value of the catch to the fisherman, for 1947, was $331,218.

Population differences.—The specimens examined make it seem possible that some population differences exist in this species with respect to the fin ray and gill raker counts, as shown by the following tabulation. These apparent differences may disappear when more specimens from the southern range of the species are examined. However, should they be found to exist in fact, differences in the fin ray counts will prove to be of some help in distinguishing this species from *aestuarius*. On account of the possible lower counts of *californicus* in the southern population the relative number of intergrades may largely or partly disappear where both species occur together. (Compare the following tabulations with tables 5 and 6.)

Anal rays

	49	50	51	52	53	54	55	56	57	58	59
Number											
San Diego frequencies	1	4	5	12	22	19	15	14	4	2	2
Lower California frequencies			1	2	4	4	2	2			

Dorsal rays

	66	67	68	69	70	71	72	73	74	75	76
Number											
San Diego frequencies	4	6	9	16	14	16	17	6	5	2	1
Lower California frequencies		1	4	2	1	2	3	1	1		

Gill rakers on upper limb

	7	8	9	10	11
Number					
San Diego frequencies	10	48	29	3	1
Lower California frequencies	4	5	1	1	

Gill rakers on lower limb

	18	19	20	21	22	23
Number						
San Diego frequencies	4	8	35	23	16	5
Lower California frequencies	1	2	1	6	1	

Pleuronectes maculosus GIRARD, Proc. Acad. Nat. Sci., Philadelphia, 7: 155, 1854 (San Diego, Calif. The name is a homonym of *Pleuronectes maculosus* CUVIER, Reg. Anim., nouv. ed., t. 2, p. 341, 1829; and may also prove to be a homonym of *Pleuronectes maculosus* GRONOW, in Cat. Fish. British Mus., edit. by Gray, p. 89, 1854, if the exact dates of publication could be ascertained).

Paralichthys maculosus GIRARD, U. S. Pacific R. R. Exp. Sur. (Zool.) 10 (Fish.): 147, 1858 (San Diego, Calif.).

Hippoglossus californicus AYRES, Proc. California Acad. Sci. 2: 29, 1859 and [p. 59] fig. 10, 1860 (San Francisco Bay).

Pseudorhombus californicus GÜNTHER, Cat. Fish. British Mus. 4: 426, 1862 (after Ayres).

Paralichthys maculosus GÜNTHER, ibid., p. 431 (after Girard).

Uropsetta californica GILL, Proc. Acad. Nat. Sci. Philadelphia, 1862: 330 (listed).

Paralichthys maculosus GILL, ibid., 1864: 197 (listed).

Uropsetta californica GILL, ibid., p. 198 (listed).

Paralichthys maculosus LOCKINGTON, Rep. Comm. Fish. California, 1878–79: 41 (Tomales Bay to San Diego).—LOCKINGTON, Proc. U. S. Nat. Mus. 2: 79, 1879 (San Francisco, Calif.).—JORDAN and GILBERT, ibid. 3: 454, 1881 (San Francisco, Monterey Bay, San Luis Obispo, Santa Barbara, San Pedro and San Diego, Calif.).—JORDAN and GILBERT, ibid., 4: 66, 1881 (Tomales Bay to San Diego).

Paralichthys californicus JORDAN and GILBERT, Bull. U. S. Nat. Mus. 16: 821, 1883 (California).

Paralichthys maculosus JORDAN, Fishery Industries U. S. (by Goode and others), sec. 1, p. 182, 1884.

Paralichthys californicus JORDAN and GOSS, Rept. U. S. Comm. Fish. 1886: 245, 1889 (Tomales Bay to San Diego, Calif.).—JORDAN and EVERMANN, Bull. U. S. Nat. Mus. 47 (3): 2625, 1898 (Tomales Bay to Cerros I.).—GILBERT and SCOFIELD, Proc. U. S. Nat. Mus. 20: 499, 1898 (Magdalena Bay, Lower California).—STARKS and MORRIS, Pub. Univ. California (Zool.) 3: 242, 1907 (San Diego Bay).—METZ, First Ann. Rep. Laguna Lab., p. 60, 1912 (Newport, Calif.).—OSBURN and NICHOLS, Bull. Amer. Mus. Nat. Hist. 35: 180, 1916 (Port San Bartholome, Ballenas Bay

[6] This difference in the seasonal abundance as between American and Mexican waters may possibly be explained by the fishermen resorting to the more remote waters off the coast of Lower California during that part of the year, either because the fish become more scarce nearer at home or for some other reason. Another possible explanation which it may be well to check in any future studies of the flounders, is that the catch in Mexican waters may also contain quantities of *aestuarius*, a species which occurs at the southern end of the coast of Lower California and which greatly resembles the California halibut.

and Magdalena Bay, Lower California).—Starks, California Fish and Game 4: 169, fig. 89, 1918.—Whitehead, Bull. Div. Fish Game California 15: 35, 1929 (gives figures of commercial catch).—Clark, ibid., 20: 54, 1930 (quantity of commercial catch).—Clark, California Fish and Game 16: 315–317, 1930.—Walford, Bull., Div. Fish and Game California 28: 138, fig. 113, 1931.—Clark, ibid., No. 32, 1931 (an account of the fishery).

Paralichthys maculosis Ulrey and Greeley, Bull. South. California Acad. Sci. 28: 31, 1928 (Santa Monica Bay, San Pedro Bay and Newport Bay, Calif.).

Paralichthys californicus Norman, Monogr. Flatfishes, p. 81, fig. 47, 1934 (San Francisco and San Diego, Calif.; Magdalena Bay).

PARALICHTHYS AESTUARIUS

Gulf flounder

(PLATE 10)

Common name.—Apparently this species has as yet no common name, and the term "gulf flounder" is proposed as its uniform common name. This name refers to its habitat, being the most common species of *Paralichthys* in the Gulf of California.

Diagnosis.—Scales ctenoid on eyed side in small specimens, cycloid in large, the gradual change in the character of the scales generally taking place in fish between 150 and 200 mm. in round figures (varies greatly with individual fish; one of the "cotypes" in the National Museum, 220 mm., still has a few weakly ctenoid scales under the bend in the lateral line, and in another fish 193 mm., no ctenoid scales could be found); scales on caudal peduncle usually the first ones to change; cycloid scales on blind side at all ages; 64 to 79. Accessory scales present, first beginning to appear in specimens of 75 to 100 mm., very numerous on both sides in specimens 200 mm. or longer. Total number of gill rakers 24 to 31, the greatest concentration of individuals at 27 or 28; 18 to 23 on lower limb; 6 to 9 on upper limb, the mode at 8. Anal rays 57 to 67; dorsal rays 75 to 85.[7] Pectoral rays predominantly 12, sometimes 13 or 11 (12 on both sides in 14 specimens, 13 in 2, 11 in 1, 12 on eyed side, and 13 on the other in 1). Origin of dorsal slightly behind anterior margin of eye in 1 specimen 78 mm.; generally over anterior margin of eye, sometimes slightly in front or somewhat behind in specimens 81 to 220 mm., a little in front of eye in 2 specimens 330 and 381 mm. Maxillary extending backward to a vertical through posterior margin of pupil in fish up to 80 or 100 mm., through hind margin of eye or slightly past in specimens 200 mm. or longer. Depth medium. Nearly as often dextral as sinistral in the specimens examined (16 fish having the eyes on the right side and 22 on the left).

Color.—In small specimens the three spots forming the large triangle are more or less ocellated in those fish having the color preserved. Other ocellated spots are frequently present, two ocellated spots, one each in the upper and lower intermediate rows, are often especially well marked, on a vertical about two-thirds the distance from the base to the apex of the large triangle; these two spots forming a quadrangle with the two anterior spots of the large triangle, and a triangle with the prepeduncular spot on the lateral line. Often spots are present in which the center of the ocellus is lacking, thus simulating "rings." The larger specimens examined, those of 185 mm. or longer, do not show any ocellated spots, but this may be due to their long immersion in preservative. The cotypes show longitudinal rows of white spots at the bases of dorsal and anal, and are also more or less profusely snowed over with smaller white spots. The other specimens examined do not show the white spots, but some have longitudinal rows of dark spots at the bases of the vertical fins in place of the white spots.

Specimens examined.—Shoal Point, at mouth of Colorado River, *Albatross*, 2 specimens, 193 and 220 mm. (48128, originally designated type), 3, 185–195 mm., same data (Stanford Univ. Zool. Coll. 195); 2, 66 and 76 mm., same locality, March 28, 1889. Gulf of California, *Albatross:* lat. 30°36′30″ N. long. 114°27′45″ W., Mar. 27, 1889, 24 fathoms, 1, 381 mm. (47280); lat. 30°58′30″ N. long. 113°17′15″ W., Mar. 24, 1889, 11 fathoms, 1, 330 mm. (47281); lat. 31°17′30″ N. long. 113°57′15″ W., Mar. 25, 1889, 10 fathoms, 1, 203 mm. (47284). The following specimens obtained by the *Pawnee* of the Bingham Oceanographic Foundation in 1926: San Felipe Bay, May 19, 3, 101–159 mm.; Gongago Bay, May 18, 9, 66–113 mm., and May 17, 10, 68–148 mm.; Angeles Bay, May 11, 1, 37 mm.; San Francisquito Bay, May 9, 3, 110–154 mm.; Conception Bay, May 1, 1, 81 mm., and May 2, 1, 80 mm. Total number of specimens studied 38, ranging 37 to 381 mm.

[7] One specimen from Gongago Bay has only 71 dorsal rays. The dorsal fin of this specimen apparently has been injured to its base, in part, and regenerated. This count was, therefore, neither included in the diagnosis nor in table 6.

Geographic distribution.—Besides the localities given above from which specimens were studied (all from the Gulf of California), the species has also been recorded from Magdalena Bay on the west coast of Lower California under the name of *Paralichthys magdalenae*. The present known range of the species is therefore from the mouth of the Colorado River to Magdalena Bay. In the latter locality it occurs together with *californicus*. It is possible that it extends further north on the west coast of Lower California and that it has been confused there with *californicus*.

Size.—The type of *magdalenae*, 17 inches, is the largest specimen known of this species. The largest specimen examined in this study is 15 inches (381 mm.).

Distinctive characters and relationship.—As far as the practical work of correctly identifying material is concerned, it is only necessary to consider the relation of the present species with *woolmani*, *californicus*, and *H. tetrophthalmus*, since these are the only known species which occur together with it in parts of its range, with which it may be confused. *P. aestuarius* may be distinguished from *woolmani* by the number of gill rakers (table 4). There is a wide gap in the ranges of the two species, and they may be separated without difficulty, at all ages, by that character alone. *H. tetrophthalmus* has a still smaller number of gill rakers. The situation becomes difficult, however, when we try to distinguish correctly *aestuarius* from *californicus*, as discussed under the account of the latter.

This species is evidently closely related to *californicus*, nearly agreeing with the latter not only in the number of gill rakers and the number of scales, but also in the almost invariably sinistral or dextral body. The change in the character of the scales of *aestuarius* with age, ctenoid in the small fish becoming cycloid in the larger individuals, furnishes evidence as to the probable phylogenetic development of some species of *Paralichthys*. Assuming that the loss of spinules on the scales is a more recent development in this genus, it may be stated that *aestuarius* is an offshoot of *californicus*. As a further development along this line of modification, *woolmani* has been derived from *aestuarius*, by the loss of scale spinules at all ages. We thus have evidence to show the derivation of the subgenus *Chaenopsetta* from typical *Paralichthys*.

Synonymy.—The species described under the name *Paralichthys magdalenae* was evidently based on a specimen of *aestuarius*. Abbott in describing his supposedly new species compared it with *californicus* and correctly pointed out the important differences, as far as the size of the specimen which he studied was concerned. However, these are the very differences which distinguish *aestuarius* from *californicus*. Gilbert and Starks, by a comparison of the types of *magdalenae* and *aestuarius* have already concluded that the former was based on a specimen of the latter. Notwithstanding that the edition of the check list by Jordan, Evermann and Clark (1930) lists *magdalenae* as a tenable species, this name should be relegated to the synonymy of *aestuarius*.

Economic importance.—No data are at present extant as to the economic importance of this flounder, if indeed, it enters the market at all. However, the species seems to be common where it does occur and it also reaches marketable size. Consequently, it seems to offer possibilities for exploitation, should it prove to occur in commercial quantities. Moreover, in view of its close resemblance to the California halibut, it is possible that it now enters the market mixed with that species in catches obtained southward, in Mexican waters.

Paralichthys aestuarius Gilbert and Scofield, Proc. U. S. Nat. Mus. 20 : 499, pl. 39, 1898 (Shoal Point, mouth of Colorado River, Mexico).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3) : 2626, 1898 (Shoal Point, Mouth of Colorado River, Mexico).

Paralichthys magdalenae Abbott, ibid., p. 2871 (Magdalena Bay, Lower California).

Paralichthys aestuarius Gilbert and Starks, Mem. California Acad. Sci. 4: 198, 1904 (type compared with *magdalenae*).

Paralichthys magdalenae Jordan and others, Rept. U. S. Comm. Fish., 1928: 223, 1930 (listed).

Paralichthys aestuarius Jordan and others, ibid., 224 (listed).—Norman, Monogr. Flatfishes, p. 82, fig. 48, 1934 (based on a paratype).—Breder[8] Bull. Bingham Ocean. Coll. 2 (3): 1936 (San Francisquito Bay, Gongago Bay, Conception Bay, San Felipe Bay, Angeles Bay, all localities in Gulf of California).—Hiyama, Marine Fishes of the Pacific Coast of Mexico. Edited by T. Kumada, p. 58, pl. 91, 1937 (Mexico).

[8] The majority of specimens forming the basis of the present account are the same as those forming the basis of this record, and I wish to express my gratitude to Dr. Breder for the opportunity of studying these specimens.

Subgenus Chaenopsetta

Chaenopsetta GILL, Cat. Fish. E. Coast North America (supp. Proc. Acad. Nat. Sci. Philadelphia, vol. 13, 1861), p. 50, 1861 (genotype *Paralichthys dentatus* (Linnaeus)=*Platessa oblonga* Storer=*Platessa ocellaris* De Kay by monotypy, both latter names cited in the original account being synonyms of *dentatus*).

Chaenopsetta GILL, Proc. Acad. Nat. Sci. Philadelphia, 1864:216 (genus first defined).

This subgenus differs from typical *Paralichthys* in having cycloid scales on both sides in large as well as in small specimens. The species comprising this subgenus seem to form a natural and related group. Its possible derivation from the subgenus *Paralichthys* through *aestuarius* to *woolmani* is suggested above (p. 301). All the known species occur on the Atlantic and Pacific Coasts of North and South America.

PARALICHTHYS WOOLMANI

(PLATE 11)

Diagnosis.—Scales cycloid on both sides at all ages, 62 to 71. Accessory scales present, beginning to appear in specimens of about 150 mm., rather sparse at a comparatively large size, usually somewhat more numerous on blind side, on either side increasing in numbers somewhat with the size of the fish. Total number of gill rakers on outer arch 16 to 20, usually 17 to 19; usually 4 or 5 on upper limb, infrequently 6; usually 13 or 14 on lower limb, sometimes 12 or 15, infrequently 11. Anal rays 55 to 60; dorsal rays 70 to 81. Pectoral rays most often 12, commonly also 11 (12 on both sides in 14 specimens, 11 on both sides in 5, 11 on blind side and 12 on the other in 2). Origin of dorsal more or less behind anterior margin of eye in specimens 60 to 90 mm., generally over anterior margin of eye in specimens 90 to 250 mm., in front of anterior margin of eye in 1 specimen 429 mm. Maxillary extending backward to underneath the space between posterior margin of eye and that of pupil in specimens under 100 mm., to a vertical through posterior margin of eye or nearly there in specimens up to 200 mm., somewhat past eye in one specimen 429 mm. Maxillary and head longer and body somewhat deeper than in the closely related *brasiliensis* when specimens of like size are compared. Sinistral.

Color.—Color pattern more distinguishable in smaller specimens. Spots, where distinct, usually in 5 longitudinal rows, sometimes more or less irregularly arranged, faintly suggesting 7 rows. Ocellated spots present, frequently numerous. Spots forming the large triangle frequently rather more prominent than other spots. Other shadings on body variable as in related species, irregularly shaded, light and dark; the intensity of the shadings variable, sometimes light all over and often very dark; ocellated character of spots in darker specimens often not discernible, sometimes snowed over with many white spots; sometimes sprinkled profusely with small dark spots; longitudinal rows of white spots along dorsal and ventral profiles sometimes more or less evident.

Specimens examined.—Carmen Island, Gulf of California (46437). La Paz, Mexico, "cotype" of *Paralichthys sinaloae* (47486). Cape San Lucas, Lower California (7036). Panama (50334). Panama City Market (78103, 81052, 81054, 81055, 81056). Taboga I., Panama (81634). Perlas I. Panama (Bingham Ocean. Coll.). Chame Point, Panama (81635, 82698). Galapagos I., Albatross; type of *P. woolmani;* about 240 mm. caudal broken at tip (47575; as to authenticity of locality of the type see following discussion). Paita, Peru (77705). Total number of specimens studied 22, 48 to 429 mm.

Geographic distribution.—The species has been recorded hitherto from localities ranging from La Paz, Sinaloa, Mexico, to Paita, Peru, and the coast of Lower California at Cape San Lucas. The material studied confirms this range and carries the distribution somewhat northward and westward within the Gulf of California to Carmen Island. The range of this species is more extensive than that of any other related species from the American continents.

The locality where the type specimen was captured is doubtful. Jordan and Bollman (1889) who first listed the specimen stated that it came from Panama. Later, presumably this same specimen was described as a new species by Jordan and Williams (1896) who now ascribe it to the Galapagos Islands, and the locality is so entered on the National Museum register. Since the species without a doubt occurs as far as Paita, Peru, it is not impossible that it extends its range to the Galapagos Islands. In regard to this question, Gilbert and Starks (1904) state, "The type of this species was collected by the Albatross in 1888, at Panama . . . Later, when made the type of a new species, it was erroneously credited to the

Galapagos Islands." These authors, however, do not indicate whether their statement is based on the original record of Jordan and Bollman, or whether they had additional unpublished information showing that the later record of Galapagos Islands is erroneous.

Size.—Jordan (1895) records it as reaching an estimated length of "about three feet" and that most specimens are "much smaller." Outside of this estimated maximum length, the largest individual which appears to have been actually measured is given by the same author as 44 cm. (17½"), taken in the estuary at Mazatlan, Mexico. Meek and Hildebrand record a maximum length of 30.5 cm. The largest specimen examined by me, which was also studied by Evermann and Radcliffe (1917), is 43 cm., from Paita, Peru.

Distinctive characters and relationship.—This species may be distinguished from all others, except *aestuarius*, of the same genus occurring on the Pacific Coast of North and South America, by its cycloid scales. From *aestuarius* which occurs in part of its range and also has cycloid scales when large, it may be separated by the fewer gill rakers: 12 to 15 on the lower limb of the first arch of *woolmani*, 18 to 20 in *aestuarius;* the frequency distribution of the gill raker count in the two species being sufficiently discontinuous to enable one to distinguish individual fish with assurance. This species is apparently most closely related to *brasiliensis* from the Atlantic coast.

Synonymy.—*P. sinaloae* described by Jordan and Abbott and recognized in the new edition of the check list should be deleted and this name placed in the synonymy of *woolmani*. The authors in describing *P. sinaloae* have correctly indicated the differences between their supposedly new species and *adspersus*, except as to the width of the interorbital which is approximately the same when specimens of similar size are compared. However, the distinguishing characters as stated by these authors are the same which differentiate *woolmani* from *adspersus*. These authors further state that *woolmani* probably differs from their *sinaloae* because of the smaller number of gill rakers of the former. The type of *woolmani* has been studied. On the eyed side it has 11 well-developed gill rakers on the lower limb; and 4 well-developed ones on the upper limb with one short, stumpy gill raker above the 4. According to my method of counting it would be enumerated as 5+11, and this is the number given in the original description. On the blind side it has 12 well-developed gill rakers on the lower limb with one very short and small but plainly perceptible gill raker in front; and 4 well-developed gill rakers with one tuberosity above. According to my method of counting they would be enumerated as 4+13. Therefore, the gill rakers of the type specimen of *woolmani*, even when the eyed side is considered, fall within the regular frequency distribution for the species here described, which also evidently includes *sinaloae* stated to have 13 or 14 gill rakers on the lower limb. One of the paratypes of *sinaloae* (U.S.N.M. 47486) has been examined, and, except for its being somewhat more slender than the average specimen of *woolmani* at that length, it does not differ from that species. Gilbert and Starks who have reexamined the types of *sinaloae* also concluded that they represent specimens of the previously described *woolmani*.

Economic importance.—This species is a food fish of some importance where it occurs. Meek and Hildebrand (1928) state it to be "rather common at Panama, and it is of some commercial value," and Gilbert and Starks (1904) report it as "abundant at Panama." Jordan (1895) states it to be "very common . . . at Mazatlan [Mexico] . . . and is a food fish of some importance." However, no figures of the catch are available by which the commercial importance of the species may be definitely established.

Paralichthys dentatus Goode and Bean (in part) Proc. U. S. Nat. Mus. 2: 123, 1879 (The specimen recorded from Paraguay, U.S.N.M. 8436, Capt. Page, agrees more nearly with *woolmani* and the recorded locality is most probably in error although the characters of the specimen are not decisively indicative.)

Paralichthys adspersus Jordan and Gilbert (not Steindachner), ibid., 5: 370, 1882 (Cape San Lucas, Lower California).—Jordan and Gilbert, Bull. U. S. Fish. Comm. 2: 108, 1882 (Mazatlan, Mexico).—Jordan and Gilbert, ibid., p. 111 (Panama).—Jordan and Bollman, Proc. U. S. Nat. Mus. 12: 182, 1889 (the locality is given as Panama, but later changed to Galapagos Is. by Jordan and Williams, 1896).—Jordan, Proc. California Acad. Sci. (2) 5: 503, 1895, (Mazatlan and La Paz, Mexico).

Paralichthys woolmani Jordan and Williams, Proc. U. S. Nat. Mus. 19: 457, 1896 (apparently based on same specimen recorded by Jordan and Bollman, 1889, as coming from Panama, but now assigned to Galapagos Islands).

Paralichthys adspersus JORDAN and EVERMANN (in part), Bull. U. S. Nat. Mus. 47 (3): 2627, 1898 (specimens from Mazatlan and La Paz refer to this species).

Paralichthys woolmani JORDAN and EVERMANN, ibid., p. 2628 (redescription of type).

Paralichthys sinaloae JORDAN and ABBOTT, ibid., p. 2872 (Mazatlan and La Paz, Mexico).

Paralichthys woolmani GILBERT and STARKS, Mem. California Acad. Sci. 4: 107, 1904 (Panama).

Paralichthys adspersus THOMPSON (in part), Proc. U. S. Nat. Mus. 50: 411, 1916 (Mazatlan, Mexico).

Paralichthys woolmani EVERMANN and RADCLIFFE, Bull. U. S. Nat. Mus. 95: 140, 1917 (Paita, Peru).—MEEK and HILDEBRAND, Publ. Field Mus. Nat. Hist. Chicago (zool. ser.) 15 (3): 974, 1928 (Chame Point, Taboga I. and Panama City market, Panama).

Paralichthys sinaloae JORDAN and others, Rept. U. S. Comm. Fish., 1928 (2): 224, 1930 (listed).

Paralichthys woolmani JORDAN and others, ibid. (listed).—NORMAN, Monogr. Flatfishes, p. 86, fig. 51, 1934 (La Paz, Mexico; Panama).—BREDER, Bull. Bingham Ocean. Coll. 2 (3): 4, 1936 (Perlas Is., Panama Bay).

Paralichthys adspersus HIYAMA, Marine fishes of the Pacific Coast of Mexico, edited by T. Kumada, p. 58, colored plate 43, 1937 (Mexico).

PARALICHTHYS BRASILIENSIS

Diagnosis.—Scales cycloid on both sides at all ages; 62 to 72. (Posterior end of curve in lateral line often not continued rather abruptly into straight horizontal part, as in related species, but somewhat gradually merging with straight part along a short rather oblique line.) Accessory scales present, usually in somewhat larger numbers on blind side, comparatively not numerous on both sides, present in specimens as small as 131 mm. (the smallest examined), sometimes still absent in specimens as large as 155 mm. Total number of gill rakers on first arch 18 to 22; 4 or 5, sometimes 3, on upper limb; 14 to 17 on lower limb. Anal rays 54 to 60; dorsal rays 68 to 78. Pectoral rays 11 in most fish, sometimes 10 on one or both sides (11 on both sides in 10 specimens; 10 on both sides in 3; 10 on blind side and 11 on the other in 2; 10 on eyed side and 11 on the other in 2). (Vertebrae 11+23 according to Thompson 1916). Origin of dorsal more or less in front of anterior margin of eye in specimens 131 mm. or longer. Maxillary about reaching a vertical through posterior margin of orbit in specimens 131 to 214 mm., somewhat past eye in larger fish. Head and maxillary rather short. Body of medium depth. Sinistral.

Color.—More or less mottled with shadings of various intensity: traces of white rather diffuse spots at bases of dorsal and anal in some specimens. No evidence of ocellated spots in the specimens examined, but probably more or less faded from long immersion in preservative. The figure published by McDonagh of a young specimen shows some ocellated spots. (The prepeduncular spot appears to be doubled in his figured specimen.)

Specimens examined and geographic distribution.—Rio de Janeiro: U. S. Exploring Expedition (83404 and 83399, the type and paratype, respectively of *Xystreurys ribeiroi*). Montevideo, Uruguay; Albatross (77388). Buenos Aires, Argentina; Albatross (77389). Mar del Plata at Necochea, Argentina, Dr. T. L. Marini. Total number of specimens studied 17, 131 to 477 mm., the localities ranging from Rio de Janeiro to Mar del Plata. The northernmost record in the literature is also Rio de Janeiro; the southernmost record is that by McDonagh, namely, San Blas, Argentina.

Distinctive characters and relationship.—As compared with related species which are known at or near its range, *brasiliensis* may be distinguished from *Pseudorhombus isosceles* and *Paralichthys patagonicus* by its cycloid scales. Two species occurring through or near its range belong to the subgenus *Chaenopsetta* and also have cycloid scales, namely, *tropicus* and *ovrax*, from both of which the present species may be distinguished by the greater number of gill rakers, and from *ovrax* it may be distinguished also by its smaller scales. In the possession of cycloid scales it agrees with 4 species from the east coast of the United States. As compared with the latter it may be separated from *dentatus* by the lesser number of fin rays, from *albigutta* by the more numerous gill rakers and scales, from *lethostigma* by having fewer fin rays and more gill rakers, and from *squamilentus* by the more numerous gill rakers and more slender body.

The relationship of *brasiliensis*, as far as may be judged by the characters studied, is evidently nearest to *woolmani* from the Pacific coast. The two species differ in the frequency distributions of a number of characters, such as the number of rays in the pectoral fin and its length, the number of gill rakers, the relative measurement of the

maxillary, head and depth. However, there is more or less intergradation in all of these structural characters. In the comparatively few specimens studied the greatest divergence is shown by the relative length of the head and maxillary in the standard length, when specimens of like size are compared (table 8); but in view of the variation of this character with the size of the fish and the few specimens available for measurement, it is doubtful whether it will prove more divergent than the other characters, after measuring a large series. In fact, the two species are so closely related that they may be distinguished only when taken in bulk, in a group of specimens. The proper identification of individual specimens would often prove quite uncertain by a study of structural differences only, unless the locality of capture be known. The relation between *brasiliensis* and *woolmani* looks very much like another example of the numerous similar cases where two species from both sides of the isthmus of Panama show small and slightly overlapping differences. While *brasiliensis* is not now positively known to occur on the Atlantic coast of Panama, it is possible that it will eventually be found there.

Economic importance and size.—The material studied by me indicates that this is probably the most common species of *Paralichthys* on the Atlantic coast of South America, and the common commercial flounder, the linguado or lenguado, on the coasts of Brazil, Uruguay, and Argentina is quite likely the present species. Berg's (1895) record of a species of *Paralichthys* reaching one meter in length, probably refers to this species. However, in view of the fact that the several species on the coast of South America apparently have not been distinguished properly heretofore, the question of its economic importance as well as the maximum size to which the present species attains must be left for future determination.

Nomenclature and synonymy.—The original description of *brasiliensis* fails to take account of important characters, and the application of that name must be attended with considerable doubt when dependent only on the original account. From the figure and description it may be gathered that Ranzani's species is sinistral, of medium depth. It has rather low vertical fins; short, symmetrical ventrals; a short pectoral; a large mouth; large teeth; a well developed anterior curve in the lateral line. It is apparently a species of *Paralichthys*. Assuming it to belong to that genus, the only substantial characters, of those investigated in detail during this study and also mentioned in the rather lengthy original description, are the number of fin rays; D. 69, A. 53, P. 11. The figure disagrees with the description in that it shows only 48 anal rays. The numbers in the vertical fins may very readily fall within the range of variation of three species now known from that region, namely, the present species, *tropicus* and *vorax*. The number of pectoral rays is one more than in the single specimen of *vorax* examined by me, but one specimen is, of course, not of decisive importance in this case. Ranzani's figure shows rather large scales, in about 50 oblique rows over the straight part of the lateral line, rather like *vorax*, but the number of scales is not mentioned in the description and in view of apparent inaccuracies shown by Ranzani's figures in general, the size of the scales of the published figure of *brasiliensis* cannot be accepted as a reliable guide. As far as I know nobody ever redescribed the type.

In view of these uncertainties, the best we can do now is to follow later revisers. Jordan and Goss (1889) were the first authors to use the name *brasiliensis* in a definite sense. They gave a recognizable description of a species of *Paralichthys* to which they applied Ranzani's name. The species described by them is evidently the same as the one described herewith and I follow these authors in their nomenclature.

Norman (1934) substitutes the name *orbignyana* for this species and applies the name *brasiliensis* to the species described by Günther, under the name of *vorax* and here so designated. This creates an unfortunate confusion of names which is possibly unnecessary. The name *orbignyana* is apparently not available for this species as discussed on pages 303 to 304. Regarding the name *vorax*, Ranzani may have had specimens of that species when he described his *brasiliensis;* but judging by the specimens examined in the National Museum and those recorded by Norman in the British Museum, the present species appears to be much more common than the one described by Günther as *vorax*, and the probabilities are much greater that Ranzani had specimens of the present species. Furthermore, the authors presenting the best accounts of this species, in addition to that of

Jordan and Goss, before the appearance of Norman's monograph, have used the name *brasiliensis* to designate it. That name apparently was generally applied to this species, although in some cases accounts of "brasiliensis" may refer partly or wholly to other species as well. Probabilities and general usage, therefore, favor the use of the name *brasiliensis* for this species, and this course is adopted here. If the type of *brasiliensis* is still in existence and in good enough condition for study this question may be settled with finality by its examination, at least as far as the use of that name is concerned.

The type and paratype of *Xystreurys ribeiroi* Fowler and Bean were examined and proved to be specimens of the common species here described.

Attention may also be called here to the use of the name *brasiliensis* by Miranda Ribeiro (Arch. Mus. Rio de Janeiro, vol. 17, 1915). That author describes his *brasiliensis* as having ctenoid scales, 5 gill rakers on the upper limb and 10 to 15 on the lower. This combination of characters does not agree with any species studied by me. Ribeiro's material either represents a new species, or it consists of a composite of more than one species.

Hippoglossus brasiliensis Ranzani, Nuov. Anal. Sci. Nat. Bologna 3: 290, 1840 (Brazil; nomen nudum).—Nov. Comm. Acad. Sci Inst. Bonon. 5: 10, pl. 3, 1842 (Brazil).

Paralichthys brasiliensis Jordan and Goss, Rept. U. S. Comm. Fish. 1886: 246, 1889 (Rio de Janeiro, Brazil; Maldonado, Uruguay).

Pseudorhombus dentatus Perugia, An. Mus. Civ. Genova (2) 10: 629, 1891 (Montevideo).

Paralichthys brasiliensis Berg, An. Mus. Nac. Buenos Aires 4: 77, 1895 (Bahia Blanca and Mar del Plata, Argentina; Montevideo and Maldonado, Uruguay; gill raker count agrees with this species but scale count more like in *vorax*).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3): 2626, 1898 (Rio de Janeiro; Maldonado).—Thompson, Proc. U. S. Nat. Mus. 50: 411, 1916 (Montevideo; Buenos Aires).

Xystreurys ribeiroi Fowler and Bean, Proc. U. S. Nat. Mus. 63 (19): 26, 1923 (Rio de Janeiro; type reexamined).

Paralichthys brasiliensis Devincenzi, An. Mus. Nac. Montevideo (2) 5: 278, 1924 (Uruguay; scale count more like that in *vorax*).—Fowler, Proc. Acad. Nat. Sci. Philadelphia 78: 273, 1926 (Buenos Aires).—Marini, Rev. Soc. Argentina Cienc. Nat. 9: 454, 1929 (Puerto Quequen, Argentina).

Paralichthys orbignyana Norman, Monogr. Flatfishes, p. 71, figs. 38 and 38a, 1934 (Rio de Janeiro; Rio Grande do Sul; Montevideo; Bahia Blanca).

Paralichthys brasiliensis MacDonagh, Rev. Mus. La Plata 34: 52, pl. 5, 1934 (Atalaya, Costa Sur, Mar Chiquita, Bahia Blanca and San Blas, Argentina).—Ginsburg, Jour. Washington Acad. Sci. 26: 132, 1936 (nomenclature discussed).

PARALICHTHYS DENTATUS

Summer flounder

(PLATE 12)

Common names.—Like other fishes this species is known by a number of common names. The early settlers, familiar with the common plaice of English waters, applied this name to the species. Thus, at about the middle of the eighteenth century, Dr. Garden who sent a specimen of the fish to Linnaeus used the name "plaise" to designate it, and that name is still in use in some sections. On the coast of New Jersey some fishermen call it splaice (Smith 1894) an evident variant of plaice. During the middle of the last century an attempt was made to introduce the name turbot for this fish on the Boston market in order to find a ready sale for it under that name which is used in England to designate another species of flatfish that is well esteemed. On Long Island it is generally called fluke, and this name is used by fishermen and especially by sportsmen in other sections also, but the same name is sometimes applied to other species of flatfishes. The name "summer flounder" is commonly used by fishermen in the more northern part of its range, because this is the common commercial flounder taken during the summer, as opposed to *Pseudopleuronectes americanus*, the common commercial species caught during the winter in the same region. The name "summer flounder" is most frequently used by writers and is here adopted as the uniform common name of the species. A summary of the other common names as compiled from the literature, and the locality in which the names are used, follows.

Summer flounder (New Jersey; New York; Rhode Island). Fluke (New York). Plaice (New York; Mass.). Chicken halibut (by some fishermen and dealers being either mistakenly or purposefully regarded as the young of the halibut which it resembles). Brail (Rhode Island). Puckermouth (Rhode Island). Turbot (Mass.). Flatfish (Long Island, New York; Chesapeake Bay; also generally applied). Flounder is applied throughout its range by many people who do not distinguish the different species of flat-

fishes. Book names applied to this species are: American turbot (Storer), long-toothed flounder (De Kay), flounder of New York (Mitchill), and common flounder (Baird).

Diagnosis.—Scales cycloid on both sides at all ages; 56 to 76, the greatest concentration of individuals between 62 and 70, the mode at 65. Numerous accessory scales present, usually beginning to appear in specimens of about 80 to 90 mm., their first appearance usually on eyed side. Total number of gill rakers on first arch ranging 16 to 24, but few specimens of those examined having less than 20: 3 to 7 on upper limb, the great majority having 5 or 6; 13 to 18 on lower limb, only a few having less than 15. Anal rays 61 to 73; dorsal rays 80 to 96. Pectoral rays mostly 12, sometimes 13 (in 10 specimens taken at random, 12 on both sides in 7, 13 in 2, and one having 8 rays on eyed side and 12 on blind side, the last probably abnormal with respect to this character). Vertebrae 11 + 30 or 31 (in 3 specimens). Origin of dorsal over or slightly in front of anterior margin of eye in large or medium-sized fish, usually slightly behind anterior margin of eye in specimens under 100 mm. Maxillary generally extending to a vertical through posterior margin of pupil in fish of 125 mm., through posterior margin of eye at 200 mm., past eye in fish over 300 mm., the backward extension of the maxillary with relation to the eye varying considerably with individual fish as well as with size. Sinistral.

Color.—Body on eyed side with numerous well marked ocellated spots in the great majority of individuals. Usually, most conspicuous ocellated spots, one each, at posterior ends of subdorsal and supra-anal rows and the prepeduncular spot on the lateral line (for terminology of spots see p. 277), the three forming the angles of an imaginary isosceles triangle. Two somewhat less conspicuous spots than the foregoing three, but more so than the other spots on body situated at anterior end of the upper and lower intermediate rows, these two spots forming with the prepeduncular spot another and larger triangle. Most spots in the 5 rows usually more or less ocellated. A number of smaller ocellated spots scattered on anterior part of body and head usually present. Specimens often quite dark in color, less frequently unusually light, the ocellated spots in such specimens, especially in the former, not so conspicuous, sometimes their ocellated character not evident altogether. The fish is capable of changing the relative intensity of the light and dark shadings in accordance with the shades of color of the background on which it rests, and this change in color shading may be induced experimentally (Mast 1916). However, the fundamental color pattern, that is, the distribution and relative intensity of the various ocellated spots may be discerned, in the great majority of cases, irrespective of the infinite variations in shadings which the fish may assume.

Young fish between 20 and 45 mm. have groups of chromatophores somewhat like those described for *lethostigma* (p. 329) overlaying the blotches on the body. The three blotches forming the large triangle are very prominent, rather more so than in *lethostigma*. These three blotches are not markedly ocellated, thus differing from specimens of *albigutta* of similar size. None of the spots in *dentatus* are distinctly ocellated in specimens between 20 and 40 mm.; although some of the spots, especially the two posterior spots which go to form the smaller triangle, in specimens between 30 and 40 mm., sometimes give a faint indication of being destined to become ocellated. These two spots at the posterior ends of the subdorsal and supra-anal rows are prominent, more so than in either *lethostigma* or *albigutta*, although they are more or less evident in the latter two species. The other blotches on the body are usually more or less diffuse. Specimens 55 mm. or longer generally show the characteristic color pattern of large fish.

Specimens examined.—Provincetown, Mass., August 1856, Putnam (5372). Mecox Bay, L. I., N. Y. (48990). Great South Bay, L. I., N. Y. (Blue Point Cove, 35907, 49020 and 49054; Fire Island, 35963). Sandy Hook Bay, N. J. (A. M. N. H. 7795). Beesleys Point, N. J. (789). Ocean City, Md. (45109). Hog Island, Va. (5885). Cape Charles, Va. (42485, 43208, 43142, and 43162). Chesapeake Bay (many localities in Maryland and Virginia). North Carolina (A. M. N. H. 5275). Hatteras, N. C. (88478). Beaufort, N. C. (15016, 51888, 51934 and many specimens in the collection of the U. S. Bureau of Fisheries). Charleston, S. C. (17121, 33168). Coosaw River, S. C. (59099). Parrot Creek, S. C. (59036). St. Simons Bay (outside), Ga. (collected by W. W. Anderson). Fernandina, Fla. (collected by the

Grampus). Total number of specimens studied in detail for the number of gill rakers, fin rays and scales, 120; many more examined in more or less detail to verify conclusions based on the above; sizes of specimens examined ranging 20 to 432 mm. Two lots of this species in the National Museum evidently were supplied with inaccurate or incomplete data as to locality, as follows: 35799, Mississippi, Lt. Wailes, 3 specimens, 193–248 mm. These specimens were possibly sent by the collector from Mississippi, but certainly not captured there. 5767, Jamaica, C. B. Adams, 1 specimen, 192 mm. The location of "Jamaica" is doubtful, but it probably refers to Jamaica Bay, Long Island, N. Y.

Geographic distribution and habitat.—The localities from which specimens were examined represent a range from Provincetown, Mass., to Fernandina, Fla. Around the northern end of Cape Cod, in Cape Cod Bay, it has been reported from North Truro (Kendall 1908) and Wellfleet (Storer 1864). In a review of the literature of the species, no authentic records north of Cape Cod were found. The distribution, Fernandina, Fla., to Provincetown, Mass., and around the point to Wellfleet, as based on material examined and on unquestionable records in the literature, must therefore stand for the present.

Kendall (1908, and Proc. Portland Soc. Nat. Hist., vol. 3, pt. 1, pp. 70 and 133, 1914) ascribes three records for Casco Bay, Maine, to the present species, one by Holmes and the other two from entries in the register book of the National Museum. The record by Holmes (in Second Ann. Rept. Nat. Hist. Geol. Maine, p. 61, 1862) as *Pomatopsetta dentata* Gill, most likely refers to the species now known as *Hippoglossoides platessoides*. At about the time when Holmes' report was published the leading American ichthyologists, such as Storer, De Kay, and Gill applied the specific name *dentata* to *Hippoglossoides platessoides*, and the type of Gill's genus *Pomatopsetta*, is that species. Moreover, *Hippoglossoides platessoides* is a common fish in the Gulf of Maine, although it is generally taken in deeper water, at 15 fathoms or beyond. Holmes lists three species of flatfishes from Maine, the other two being *Hippoglossus americana*, the halibut, and *Pleuronectes americanus*, the winter flounder, both common species. It is, therefore, much more likely that his *Pomatopsetta dentata* Gill was based on material of *Hippoglossoides platessoides* rather than on *Paralichthys dentatus*. As to the two records on the register of the National Museum, they probably also refer to some other common species of flatfish. During the seventies when the identifications entered on the register were presumably made, *Paralichthys dentatus* was known among the American ichthyologists under the specific name of *ocellaris* rather than *dentatus*. According to the data now extant, *Paralichthys dentatus* does not occur north of Cape Cod.

The species is very common and caught in commercial quantities from Cape Cod to North Carolina, and is abundant from southern Massachusetts to Chesapeake Bay. In Chesapeake Bay it is the most common flatfish marketed. In the summer it is found chiefly in shallow water, generally to about the 15 fathom line and, in the winter, on the coast of the northern States, it lives in deeper water, and has been recorded from a depth of 100 fathoms off the coast of Virginia, March 3, 1929 (Schroeder 1931). The species shows a preference for hard or sand bottom, but is also taken on mud or grass bottoms.

Size.—The usual sizes of this species which enter the market range from 12 to 25 inches, having a weight of ½ to 6 pounds. Fish more than 6 pounds are not common. The largest specimen on record weighed 30 pounds, taken off Fishers Island, N. Y. (Nichols and Breder 1927). Goode (1884) records the capture of a specimen weighing 26 pounds, landed at Noank, Conn. A half-pound fish measures about 12 inches; 1 pound, about 15 inches; 2 pounds, about 18 inches; 3 pounds, about 20 inches; 4 pounds, about 22 inches; 8 pounds, about 27 inches; 10 pounds, about 30 inches.

Distinctive characters and relationship.—The characteristic color pattern of this species enables one to identify the great majority of specimens at a glance. Near the northern end of its range, at Cape Cod, dark specimens in which the color pattern is not well marked, resemble somewhat *Hippoglosoides platessoides*, but this latter species may be readily distinguished by its eyes and color being on the right side, its lack of a high arch in the anterior part of the lateral line, its smaller

mouth, smaller teeth, ctenoid scales, and other salient differences. Some difficulty may be encountered in properly distinguishing scattered specimens of this species from *albigutta* or *lethostigma* where their ranges overlap. Doubtful specimens of *dentatus* in these localities may generally be properly placed by the more numerous gill rakers. For separating the residual few specimens in which the number of gill rakers approach the other two species see page 282. The three species are evidently quite closely related.

Bionomics

Spawning period.—The spawning period of this species is evidently the late fall and winter possibly extending to early spring in Chesapeake Bay, judging by available evidence. Hildebrand and Schroeder (1928: 166) found specimens taken in Chesapeake Bay during October, having comparatively large gonads. Hildebrand (op. cit.) found the gonads of fish taken at Beaufort, N. C., to be partly developed during fall and early winter while those taken in March and April were fully spent. Abundant data on the size of the fry and its bearing on the spawning season of the species is furnished by Hildebrand and Cable (1930: 470).[9] In the very extensive collections made at Beaufort, N. C., and reported on by these investigators, individuals 25 mm. (1 inch) or less in length were taken from September to May, the bulk of the specimens having been collected in November and December. As three common species occur at Beaufort, N. C., and no characters for separating the very young fry, before the fin rays and gill rakers become differentiated, are known at present, only the approximate spawning period for the separate species may be surmised. It is possible that the height of spawning varies with the different species. If that is the case, the spawning periods of the separate species probably overlap to a large extent, since the data published by Hildebrand and Cable do not show any dominant concentration of fry at different periods of time, when grouped by month intervals. (Perhaps, in a grouping of data by smaller intervals of time differing heights of spawning would show up to some extent.) In Chesapeake Bay spawning apparently takes place later, in the late winter or early spring, if we are to judge by the size of the fry in relation to the season of the year when taken. Thus, Hildebrand and Schroeder (op. cit.) report fry taken there in May and June to be approximately 25 mm. (0.9 to 1.1 inches). During 1892 the *Grampus* made some collections in Chesapeake Bay of young *Paralichthys dentatus* which are now preserved in the National Museum as follows: June 28, 3 specimens, 49, 58 and 83 mm.; June 29, 1 specimen, 40 mm.; July 4, 2 specimens, 38 and 50 mm.; July 6, 2 specimens, 42 and 45 mm.; July 16, 1 specimen, 57 mm. A comparison of the measurements of these few specimens with the extensive data given by Hildebrand and Cable seems to indicate that spawning occurs somewhat later in Chesapeake Bay.

Spawning places and distribution of fry.—In regard to particular situations where spawning takes place, Bigelow and Welsh (1925: 494) and Hildebrand and Schroeder (1928: 166) suggest the possibility of the fish going to deep water to spawn. There is evidence showing a general migration of the fish to deeper water with the advent of cold weather (p. 320). One of the objects of this migration may be spawning. That spawning takes place offshore is further indicated by the distribution of the fry as found by Hildebrand and Cable (1930: 474). Fry up to 3 mm. were taken only at sea; somewhat larger ones, up to 5 mm., were taken also within Beaufort Harbor, but they were much more numerous outside Beaufort inlet; while specimens 6 to 10 mm. are about equally distributed in the inner and outer waters, extending from 12 to 15 miles offshore into the estuaries of Newport and North Rivers. This furnishes evidence of a gradual movement of the fry to the inner waters from offshore where they hatch.

The type of eggs is unknown at present, but it is probably demersal, as recently hatched fry were taken by Hildebrand and Cable (1930: 475) chiefly on the bottom. If they hatch on the bot-

[9] The most extensive studies on the biology of *Paralichthys* which have been carried out so far, are those by Hildebrand and Cable to whose report the reader is referred for detailed accounts. These authors made their studies at Beaufort, N. C. Since, however, three closely related species of *Paralichthys*, are common there, and it is difficult or impossible to separate the fry by species, Beaufort is not a favorable place to study the development of *dentatus*. The Chesapeake Bay region and localities farther north are more suitable because only this one species of *Paralichthys* occurs there.

tom, the young become distributed to some extent in the upper layers after hatching and are taken also at the surface with tow nets, but most of them remain on the bottom.

Growth.—The rate of growth of this species is as yet unknown, no special study having been made based on a sufficient amount of material. Hildebrand and Schroeder (1928: 166) by measuring a limited number of available specimens give tentative figures for growth as being 4½ to 7 inches at 1 year and about 10 inches at 2 years. The age at which the fish mature is likewise unknown. Hildebrand and Cable state (1930: 475) that individuals with roe which have been observed were large, 16½ to 29 inches. The age of specimens of that size is unknown at present.

Migration.—During the warmer months of the year, between April or May and November or December, depending on the latitude, this species is readily taken in comparatively shallow water, generally between 2 and 20 fathoms. With the advent of cold weather it becomes scarce in shallow water, indicating a general migration of the fish to deeper water. During the winter months it may be taken in large numbers beyond the 20 fathom line (Pearson 1932) and down to 100 fathoms (Schroeder 1931). This migration is evidently induced by the inability of the fish to withstand the colder temperature of the more shallow water. Fish sometimes are found torpid in shallow water during the winter (Baird 1855), probably being trapped by a sudden chill after being lured from greater depths by a spell of warm weather. The movement to deeper water during cold weather is a common habit of various species of fish. In the case of the summer flounder this is apparently also a spawning migration. The fish appear again in shallow water during the spring of the year, the time of appearance varying with the latitude, and most probably also with the temperature conditions during any given year. Other mass migrations of the adults are unknown, and it is unlikely that the species makes any other general migrations. The summer flounder is probably a comparatively immobile fish as a species. The young fry after hatching remain chiefly on the bottom, but they become also distributed in the upper layers to some extent, as stated. The fry undertake a movement from offshore to the inner waters. After the young fish exceed a length of 10 mm. they stay on the bottom and continue to move inshore, many going into the estuaries of rivers for considerable distances. The young evidently remain at the brackish-water zone and grow till they reach a length of about 125 mm. when they seem to gradually spread toward salt water.

Food and feeding habits.—The summer flounder is primarily a predaceous fish. Its food consists chiefly of such species of fish and small invertebrates as are readily accessible in the region which it inhabits. The following fishes have been reported as being preyed upon by the summer flounder, namely, mackerel, menhaden, tautog, sand launce, silversides, butterfish, and scup; of invertebrates, crabs, shrimp, squid, small mollusks, worms, and sand dollars. In the business of obtaining food it is aided by its ability of partial concealment; by simulating the color of the background, by partly burying itself in the bottom, and by the natural flat shape of the body. It lies flat on the bottom, often partly buried in the sand or mud, with the light and dark shades of color of the uppermost surface so varied in intensity on different parts of the body as to blend and harmonize with the background. The instinctive concealment is often so well accomplished that it is quite hard to detect the position of the fish even when keeping a sharp lookout in fairly clear water. It thus waits till some unwary victim chances its way when it strikes with swiftness and force. Sometimes it will pursue schools of small fish to the very surface.

Races.—While it is not the primary aim of this investigation to elaborate in detail the characters which may be used in separating races, and, moreover, the material at hand is not sufficient for a thorough racial analysis; it is yet desirable to point out the bearing of the characters investigated on the study of racial differentiation. The material examined yields evidence that the populations of *Paralichthys dentatus* from Chesapeake Bay and from Beaufort, N. C., belong to two distinct racial stocks. The frequency distributions of the meristic characters given in tables 2 to 6, segregated by locality, for *dentatus*, are as follows:

Gill rakers on upper limb

	3	4	5	6	7
Class					
Chesapeake Bay frequencies	--	--	31	35	5
North Carolina frequencies	2	4	29	6	1

Gill rakers on lower limb

	13	14	15	16	17	18
Class						
Chesapeake Bay frequencies	--	--	9	28	25	9
North Carolina frequencies	4	2	9	15	7	2

Total number of gill rakers on outer arch

	16	17	18	19	20	21	22	23	24
Class									
Chesapeake Bay frequencies	--	--	--	--	6	19	15	23	8
North Carolina frequencies	2	2	1	2	6	15	5	6	--

Anal rays

	61	62	63	64	65	66	67	68	69	70	71	72	73
Class													
Chesapeake Bay frequencies	--	--	--	1	3	6	17	12	6	11	3	6	5
North Carolina frequencies	1	1	--	2	1	7	6	8	6	7	3	--	--

Dorsal rays

	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
Class																	
Chesapeake Bay frequencies	--	--	1	--	2	7	5	8	12	12	10	4	3	2	3	--	1
North Carolina frequencies	1	1	--	4	--	1	3	4	8	9	4	1	2	2	--	1	--

The data tabulated show that there is one consistent and statistically measurable character which may be used in racial studies, namely, the number of gill rakers. There is only a slight difference in the frequency distribution of the fin ray counts, which is somewhat more pronounced in the anal ray count. However, while the difference in the anal count is not very significant, it is of considerable practical value in identification, since overlapping specimens at the extreme end of the frequency distribution disappear in northern specimens, and *dentatus* from Chesapeake Bay is thus more readily separable from *albigutta*. There is practically no difference in the scale count which is, on that account, omitted from the preceding tabulations by locality. The racial difference in proportional measurements, shown in table 8, in groups of specimens of approximately like sizes, is not pronounced. The North Carolina population of *dentatus*, in general, is somewhat deeper bodied and has a slightly longer head and maxillary. These differences do not hold in all the size groups, and it is possible that curves representing the relative changes with size in these measurements will have somewhat different forms, but not enough specimens have been measured to draw any definite conclusions.

The divergence of the races of *dentatus* is such that the population from North Carolina more nearly approaches that of *albigutta* than specimens from Chesapeake Bay approach that species. When *dentatus* from Chesapeake Bay is compared with *albigutta* there is a comparatively wide gap between them as far as the total number of gill rakers is concerned, and individual specimens of the two species may be readily distinguished on that basis; but this structural gap disappears between the two species at North Carolina (compare the tabulated racial data of *dentatus* with tables 2 to 4). To a lesser extent this is also true of the anal rays.

It is to be noted, also, that there is a difference in the regularity of the frequency distributions of the number of gill rakers in the two populations of *dentatus*. The Chesapeake Bay population is more uniform in its structural characters, the spread and form of the frequency distribution is rather compact and regular; while the North Carolina population is more variable, the spread being more extensive, and the frequency polygon will assume a skewed form.

Hybridism.—The somewhat irregular frequency distribution of *dentatus* from North Carolina may possibly be due to the presence of hybrid specimens which are intermediate in some respects. This

would seemingly partly explain the cause of the difficulty of referring occasional individual specimens from that coast to their proper species. For instance, the two border-line specimens discussed above (p. 282) having a high fin-ray count, near the extreme of the distribution of the genus as a whole, and gill rakers in intermediate numbers, might be hybrids between *dentatus* and *lethostigma* (see also fig. 4). However, it is evident from the form of the frequency distributions that the number of hybrids, if indeed any do occur, are not numerous. In any case, it would require more detailed studies to prove the presence of hybrids and to show how they may be identified. It should be emphasized that the only substantial evidence showing the probable existence of hybridism consists of a rather slight irregularity in the frequency distributions of the characters studied. This evidence is certainly not conclusive. On the contrary, irregularity of frequency distributions appears to be the rule rather than the exception in nature. No evidence of hybridism between *lethostigma* and *albigutta* was found on the Gulf coast where those two are the only common species.

Economic importance.—The summer flounder is one of the important food fishes. The meat is of excellent quality and generally esteemed, resembling in flavor the halibut. It is taken chiefly during the warmer months of the year, between April and November, from shallow water to a depth of about 20 fathoms, the bulk of the commercial catch being captured between 5 and 15 fathoms. As may be expected from its bottom living habit, it is taken in the greatest numbers by the gear most suitable for taking bottom fish, by trawls. Large numbers are also taken in stationary gear, such as pound nets, fyke nets, weirs, and traps. Considerable quantities are taken by baited hook and line and to a lesser extent also by haul seines. As stated, the catch of this species had been confined chiefly to the months of April to November. Within recent years a special winter trawl fishery has developed off the coasts of Virginia and North Carolina which during the winter of 1930–31 produced a yield of this species of more than a million pounds (Pearson 1932).

The recent annual yield of this species, in round figures, is 13 million pounds, worth $2,156,000 to the fishermen. These figures are obtained by adding the statistics compiled by the Fish and Wildlife Service for "fluke" from Massachusetts to Delaware and those under the heading of "flounder" for Maryland and Virginia. The name "fluke" refers to the present species. The catch of "flounder" in the latter two States consists chiefly of *Paralichthys dentatus*, but includes a variable, an unknown percentage of *Pseudopleuronectes americanus*, which is greater in the Maryland catch and smaller in that of Virginia. The statistics used are those for 1945 for New Jersey and Delaware and for 1946 for the other States.

Synonymy.—The following involved synonymy of this species appears to be correct, as indicated by the accounts of authors. In a few cases, the specimens on which the records are based were examined. Attention may be called again to the fact that some early accounts by American writers employing the specific name *dentatus* for a flatfish (see, for instance, Storer in Hist. Fish. Mass., p. 197, pl. 30, fig. 3, 1867), refer to *Hippoglossoides platessoides*, and that the inclusion of such references by later writers in the synonymy of this species is erroneous.

Pleuronectes dentatus Linnaeus, Syst. Nat., ed. 12, pt. 1, p. 458, 1766 (Carolina).

Pleuronectes lunatus Linnaeus, ibid., p. 459 (not *Pleuronectes lunatus* L. of the tenth edition Syst. Nat., according to Günther 1861 and Goode and Bean 1885).

Pleuronectes dentatus Walbaum, Gen. Pisc., p. 116, 1792 (Carolina).—Bloch and Schneider, Sys. Ichth., p. 156, 1801 (North America).—Mitchill, Tr. Lit. Phil. Soc. New York 1: 390, 1815 (New York).

Pleuronectes melanogaster Mitchill, ibid. (New York, based on a teratological specimen).

Pleuronectes aquosus Storer (not Mitchill), Boston Jour. Nat. Hist. 1: 352, 1836 (Massachusetts).

Rhombus aquosus Storer (not Mitchill), ibid., 2: 484 (Rep. Fish. Mass., p. 146) 1839 (Boston market).

Platessa oblonga De Kay (not Mitchill), Zool. New York, Fishes p. 299, pl. 48, fig. 156, 1842 (New York).

Platessa ocellaris De Kay, ibid., p. 300, pl. 47, fig. 152, 1842 (New York).

Platessa oblonga Linsley (not Mitchill), Amer. Jour. Sci. Art. 47: 72, 1844 (Stratford, Conn.).—Storer, Proc. Boston Soc. Nat. Hist. 1: 194, 1844 (teratological specimen, no locality).—Storer Mem. Amer. Acad. Art. Sci. (n. s.) 2: 477, 1846; also in Syn. Fish. North America, p. 225, 1846.

Platessa ocellaris Baird, 9th Ann. Rep. Smithsonian Inst., p. 349 (1854) 1855.

Chaenopsetta oblonga Gill, Cat. Fish. North America (supp. Proc. Acad. Nat. Sc. Philadelphia 1862), p. 50, 1861.

Chaenopsetta oblonga var. *ocellaris* Gill, ibid.

Pseudorhombus dentatus GÜNTHER (in part), Cat. Fish. British Mus. 4: 425, 1862 (states that type of *dentatus* still in existence).

Pseudorhombus oblongus GÜNTHER, ibid., p. 426 (after De Kay).

Pseudorhombus ocellaris GÜNTHER, ibid., p. 430 (after De Kay).

Platessa oblonga STORER (not Mitchill), Mem. Amer. Acad. Art. Sci. Boston 8: 395, pl. 31, fig. 2 and 2b, 1864; also in Hist. Fish. Massachusetts p. 202, 1867 (Provincetown and Wellfleet, Mass.).

Chaenopsetta ocellaris GILL, Proc. Acad. Nat. Sci. Philadelphia, 1864: 218 (Beesleys Point, N. J.; New York; Norfolk, and Old Point, Va.).—ABBOTT, Geol. New Jersey by G. H. Cook, app. E. p. 817, 1868 (New Jersey).—VERRILL, Amer. Nat. 5: 399, 1871 (Great Egg Harbor, New Jersey).

Pseudorhombus melanogaster LYMAN, Sixth Ann. Rep. Comm. Inland Fish. Massachusetts, p. 47, 1872 (Waquoit, Mass.).

Chaenopsetta ocellaris BAIRD, Rept. U. S. Comm. Fish. 1871–72: 823, 1873 (Woods Hole, Mass.).—UHLER and LUGGER, Rep. Comm. Fish. Maryland, Jan. 1, 1876, p. 96, 1876 (Chesapeake Bay).

Chaenopsetta oblonga UHLER and LUGGER, ibid. (Chesapeake Bay).

Chaenopsetta ocellaris UHLER and LUGGER, ibid., January, 1876, p. 80, 1876 (Chesapeake Bay).

Chaenopsetta oblonga YARROW, Proc. Acad. Nat. Sci. Philadelphia 1877: 206 (North Carolina; states "occasionally taken of large size" and probably refers to *dentatus*, wholly or in part, the species of flounders not properly differentiated by this author).

Chaenopsetta ocellaris YARROW, ibid. (North Carolina, one specimen reexamined).

Pseudorhombus ocellaris JORDAN and GILBERT (in part), Proc. U. S. Nat. Mus. 1: 370, 1879 (Beaufort, N. C.).

Pseudorhombus dentatus JORDAN and GILBERT (in part), ibid. (Beaufort, N. C.).—GOODE and BEAN (in part), ibid. 2: 123, 1879 (four species confused in this account, the three common species of the east coast of the United States and one apparently erroneously said to have come from Paraguay).—GOODE and BEAN, Bull. Essex Inst. 11: 7, 1879.—BEAN (in part), Proc. U. S. Nat. Mus. 3: 79, 1880 (Noank, Conn.; Woods Hole, Mass.; Crisfield, Md. The other localities given probably contain more than one species, since this author did not properly differentiate the species).

Paralichthys ophrys JORDAN and GILBERT, Bull. U. S. Nat. Mus. 16: 822, 1883 (Charleston, S. C.).

Paralichthys ocellaris JORDAN and GILBERT, Proc. U. S. Nat. Mus. 5: 617, 1883 (Charleston, S. C.).

Paralichthys dentatus BEAN, Rept. U. S. Comm. Fish. 1882: 340, 1884 (Woods Hole, Mass.).—GOODE (in part), Fish. Ind. U. S., sec. 1, p. 178, 1884 (not the figure; an account of the fishery; includes more than one species, the geographical distribution given being erroneous).

Pleuronectes dentatus GOODE and BEAN, Proc. U. S. Nat. Mus. 8: 197, 1885 (type reexamined and described).

Pleuronectes lunatus GOODE and BEAN, ibid. (specimen described by Linnaeus as *Pleuronectes lunatus* in the twelfth edition of Systema Naturae reexamined and found to be a *dentatus*).

Paralichthys dentatus JORDAN, Proc. U. S. Nat. Mus. 9: 29, 1886 (Beaufort, N. C.).—BEAN, Bull. U. S. Fish. Comm. 7: 135 (1887) 1889 (Ocean City, N. J.).—JORDAN and GOSS, Rept. U. S. Comm. Fish. 1886: 246, 1889 (Cape Cod to Florida).—BEAN, Proc. U. S. Nat. Mus. 14: 85, 1891 (Cape Charles City, Va.; Point Lookout and St. Jerome, Md.).—BEAN, 19th Rept. Comm. Fish., New York, p. 246, pl. 2, fig. 2, 1891 (Long Island).—SMITH, Bull. U. S. Bur. Fish., 10: 72, pl. 20, 1892 (Potomac River, Md.).—RATHBUN, Rept. U. S. Comm. Fish., 1889–91: 161, 1893.—MOORE, Bull. U. S. Fish Comm. 12: 363, 1894 (Sea Isle City, N. J.).—SMITH, ibid., p. 379, 1894 (New Jersey).—BEAN, Bull. Amer. Mus. Nat. Hist. 9: 372, 1897 (Gravesend Bay, N. Y.).—JORDAN and EVERMANN, Bull. U. S. Nat. Mus. 47 (3): 2629, pl. 373, fig. 922, 1898 (Cape Cod to Florida).—SMITH, Bull. U. S. Bur. Fish., 17: 108, 1898 (Woods Hole, Mass.).—BUMPUS, Thirtieth Ann. Rept. Comm. Inland Fish. Rhode Island, p. 53, 1900 (Narragansett Bay, R. I.).—BEAN, 52 Ann. Rept. New York State Mus., vol 1, p. 110, (1898) 1900 (Long Island, N. Y.).—BEAN, 6th Ann. Rept. Forest Fish Game Comm. New York [Cat. Fish. Long Island], p. 472, 1902 (Long Island, N. Y.).—BEAN, 7th Rept. Forest Fish Game Comm. New York [Food and Game Fish., New York], p. 455, 1903 (Long Island, New York).—BEAN (in part), Cat. Fish. New York, p. 717, 1903 (Long Island, N. Y., part of the description refers to *lethostigma*).—SHARP and FOWLER, Proc. Acad. Nat. Sci. Philadelphia 56: 512, 1904 (Nantucket, Mass.).—FOWLER, Ann. Rept. New Jersey State Mus., 1905: 393, 1906 (not the figure; New Jersey, many localities given).—LINTON, Bull. U. S. Bur. Fish. 24: 410, 1905 (parasites of the species at Beaufort, N. C. Author states that material probably not well differentiated as to species).—FOWLER, Ann. Rept. New Jersey State Mus., 1906: 341, 1907 (Sea Isle City, N. J.).—SMITH, Fish. North Carolina, p. 386, fig. 178, 1907 (Beaufort, N. C.).—KENDALL, Occasional Papers Boston Soc. Nat. Hist. 7 (8): 146, 1908 (Chatham, North Truro and Menemsha Bight, Mass.; off Stratford Point and Middle Ground, Conn.; regarding record from Casco Bay, see p. 318).—EVERMANN and HILDEBRAND, Proc. Biol. Soc. Washington 23: 163, 1910 (St. George Island and Hampton Creek, Potomac River).—TRACY, Rept. Comm. Inland Fish. Rhode Island, 1910: 161 (Rhode Island).—KENDALL, Rept. Comm. Fish Game Massachusetts, 1910: 151, 1911 (Tisbury Great Pond, Mass.).—SUMNER, OSBURN, and COLE, Bull. U. S. Bur. Fish. 31 (1): 163, chart 207, 1913 (Woods Hole, Mass.).—FOWLER, Occasional Papers, Mus. Zool. Univ. Michigan 56: 19, 1918 (Cape Charles City, Magothy Bay and Smith Island, Va.).—BREDER, Zoologica, 2: 350, 1922 (Sandy Hook Bay, New Jersey).—BIGELOW and WELSH, Bull. U. S. Bur. Fish. 40 (1): 491, fig. 249, 1925.—NICHOLS and BREDER, Zoologica 9: 176, fig., 1927 (New York).—HILDEBRAND and SCHROEDER, Bull. U. S. Bur. Fish. 43 (1): 165, fig. 86, 1928 (Chesapeake Bay, many localities).—HILDEBRAND and CABLE, Bull. U. S. Bur. Fish. 46: 464, figs., 1930. (an extensive account of natural history at Beaufort, N. C.).—SCHROEDER, Copeia, 1931: 45 (off Virginia, lat. 37°36′

N., long. 74°17′ W., 100 fathoms).—Pearson, U. S. Bur. Fish. Invest. Rept. 1 (10) : 24, 1932 (an account of the winter trawl fishery off Virginia and North Carolina; those obtained in N. C. most probably contain an admixture of *P. lethostigma*).—Norman, Monogr. Flatfishes, p. 72, fig. 39, 1934 (Woods Hole, Mass.; Hampton Roads; Charleston Harbor, S. C.; reviewed).

PARALICHTHYS ALBIGUTTA

Sand Flounder

(PLATE 13)

Common name.—This species is most generally termed "flounder" by fishermen and others without any qualifying adjective, not being distinguished from related flounders. However, some fishermen on the Gulf coast are able to distinguish this species from *P. lethostigma*, the other common species of the Southern States. When so distinguished the term "sand flounder" is sometimes applied to *albigutta* and "mud flounder" to *lethostigma*, evidently alluding, correctly, to the bottom on which the bulk of each species, respectively, is taken. This suggests an appropriate uniform common name for the species. In this connection it is also interesting to note that Smith (1907) gives the names "mud flounder" and "sand flounder" as being used by the fishermen at North Carolina for *P. dentatus*. It seems possible that some fishermen at North Carolina also distinguish between the species of *Paralichthys* under those names.

Diagnosis.—Scales cycloid on both sides at all ages; of medium size, 47 to 60, nearly all specimens have 49 to 57, the apex of the curve at 52 and 53. Accessory scales present on both sides, quite numerous in large fish, beginning to appear in specimens of about 85 mm. Total number of gill rakers on first arch ranging 11 to 15, 12 to 14 in the great majority of specimens; 2 or 3, rarely 4, on upper limb; 9 to 12 on lower limb, 10 or 11 in the large majority of specimens. Anal rays 53 to 63; dorsal rays 71 to 85. Pectoral rays usually 11, sometimes 10 or 12 (11 on both sides in 10 specimens; 10 in 1; 10 on blind 11 on eyed side in 1; 10 on eyed side 11 on blind side in 1; 11 on blind side 12 on eyed side in 3). Origin of dorsal usually somewhat in front of anterior margin of eye, over anterior margin in young fish, at about 80 mm. Posterior extremity of maxillary attains to a vertical through posterior margin of pupil in specimens under 75 mm., to the space beneath the posterior margin of pupil to posterior margin of eye in specimens up to 125 mm., usually to posterior margin of eye in specimens up to 250 mm., usually to somewhat behind posterior margin of eye in specimens over 300 mm., at any given size also varying considerably with individual fish. Sinistral.

The depth, and the length of the head and maxillary in this species is evidently subject to considerable individual variability and it requires the measurement of many specimens to definitely establish the normal change of form with age. Judging by the specimens measured (table 8, p. 279), it seems that unlike the condition in *lethostigma* fish under 50 mm. are relatively more slender than somewhat longer fish. The depth increases with length in fish up to about 125 mm. The tempo of increase in body-length is then greatly accelerated, and fish between 125 and 200 mm. in length become gradually more slender. Between 200 and 300 the depth again increases. Finally, what seems to be unlike the change of growth with size in most other species of the genus, fishes over 300 mm. again show a considerable decrease in relative depth of body. Comparing *albigutta* with *lethostigma* we have the surprising fact that whereas fish under 200 mm. are definitely deeper-bodied in the former species, those over 300 mm. are markedly deeper in the latter.

Color.—The typical 5 longitudinal rows of spots more or less evident, diffuse. Most prominent spots on body, three in number, the prepedunclular spot and two at anterior ends of the two intermediate rows, forming the angles of an imaginary scalene triangle; these three spots conspicuous and ocellated in the great majority of individuals, sometimes rather faint. Other spots on body fainter and mostly not ocellated; sometimes one or more ocellated spots at posterior end of subdorsal row, less frequently at posterior end of supra-anal row, and rarely at middle of intermediate rows. Body variously shaded with light and dark hues. Frequently quite light and sometimes notably dark, the ocellated character of the three spots in such specimens sometimes faint, but these spots nearly always rather more prominent than the other blotches on the body. Individuals frequently snowed over densely with white spots, tending to disappear after death but frequently persistent in preserved specimen. This species, like *dentatus*, is able to change the relative inten-

sity of the shadings on the body to accord with its background as has been shown experimentally by Mast (1916). However, the three characteristically placed, prominent, more or less ocellated spots are usually plainly evident as may be seen by examining some of the plates published by the author.

The color pattern of *albigutta* and *dentatus* are nearly alike. There is a difference in the color of the two species, but the difference is more a matter of relative intensity of pigmentation. In *dentatus* the ocellated spots are generally more numerous. In *albigutta*, in the great majority of specimens, only three ocellated spots are present forming the large triangle, the spots forming the small triangle being absent or faint. In *dentatus* the large triangle is also present, but the spots forming the small triangle are usually the most prominent.

In young fish examined, the three characteristic ocellated spots forming the large triangle are distinct in those as small as 17 mm. and resemble those of the adults. The aggregations of coarse chromatophores overlaying the blotches which are present in *lethostigma* and *dentatus* are absent or very sparsely developed in *albigutta*. The other spots on the body are already present in fish between 17 and 30 mm. in the form of small specks in five longitudinal rows, becoming large and diffuse in fish over 30 mm.

Specimens examined.—South Atlantic Coast (36892). North Carolina (A. M. N. H. 3296). Cape Lookout (A. M. N. H. 4381 and 5280) and Beaufort (93512; A. M. N. H. 1883; many specimens from the collection of the U. S. Bureau of Fisheries Biological Station), N. C. Coosaw River, S. C. (93513). Florida (4887; U. S. and Mexican Boundary Survey; the specimen recorded as *albigutta* in a table of measurements by Goode and Bean, 1879). Key West, Fla., (specimens collected by the staff of the Fisheries Biological Station; inseparably mixed with those from Beaufort). Southern Florida (A. M. N. H. 2897). Southwest Florida (A. M. N. H. 2445). West Florida (5156). Caxambas (A. M. N. H. 2544). Tampa Bay (84041). Cedar Keys (35085), Apalachicola Bay (collected by me), and Pensacola (30818 collected in Laguna Grande by S. Stearns, Jordan and Gilbert's type of *albigutta;* 30191; 30698; 30842; specimens collected by me). Fla. Off Breton Island, La. (collected by Stewart Springer). Harbor Island, Hog Island, and Corpus Christi Pass, Tex., (collected by John C. Pearson). Total number of specimens studied in detail for the meristic characters 111; many more examined to verify conclusions; those examined ranging 17–389 mm.

Geographic distribution and habitat.—The range of the specimens examined extends from Cape Lookout, N. C., to Corpus Christi Pass, Tex., and this represents the extremes of its range, as now established, having been known previously from Beaufort, N. C., to Pensacola, Fla. The range of the species is continuous with respect to geographico-zonal variations in the environment and includes the semitropical surroundings at the southern tip of Florida. On the other hand, its range seems to be discontinuous with respect to the nature of the bottom. This species prefers hard or sandy bottoms, and where long stretches of coast having a mud bottom occur, it is either absent or rare. For instance, in my investigations during 1930, in 5 weeks of intensive and almost daily collecting on the coast of Louisiana, chiefly in the immediate vicinity of Grand Isle and extending from Bastian Island to Isle Derniere, during late June, July, and early August, not a single specimen of *albigutta* was obtained, while, at the same time, *lethostigma* was abundant and the majority of trawl landings yielded some specimens of the latter species. Soon after leaving Grand Isle and going to Pensacola about the middle of August, the first three flounders obtained there while seining in Big Lagoon, were *P. albigutta*. The bottom in the latter body of water consists largely of fine white sand, while on the coast of Louisiana, between the points indicated above, the bottom is chiefly of blue mud. The apparent conclusion which may be drawn from these observations is that the species prefers a sandy bottom.

This conclusion was further corroborated during 1932 by observations made in Apalachicola Bay, Fla. That body of water has long stretches of hard or sand bottom alternated with a mud bottom, and is a favorable location for a study of the difference in habitat of *albigutta* and *lethostigma*. Specimens of *Paralichthys* obtained there on a hard bottom are chiefly *albigutta* and those on a mud bottom are largely *lethostigma*.

as may be illustrated by the following data from my note book of three drags with a commercial shrimp trawl on June 16, 1932, in Apalachicola Bay, just off St. George Island, near West Pass. The first drag of the trawl lasting 1 hour, on a muddy bottom with occasional patches of sand, yielded, among other fishes, 7 specimens of *Paralichthys lethostigma*, 20 to 28 cm., and 2 *P. albigutta* 14.5 and 15 cm. After the first trawl was landed it was immediately put overboard and the drag continued in the same direction but on a stretch where the bottom was chiefly hard. The second drag lasted 30 minutes and the yield of *Paralichthys* was 11 specimens of *albigutta*, 9 to 21.5 cm., and 2 *lethostigma*, 19.5 and 23.5 cm. A third drag lasting 45 minutes, begun approximately at the point where the preceding drag was ended and continued in the same direction, the bottom having changed again to mud, yielded 3 specimens of *P. lethostigma*, 22.5 to 29.5 cm. and none of *albigutta*. These observations made in Apalachicola Bay were corroborated, in a general way, on numerous other occasions. The species seems to be common throughout its range where the bottom is favorable for its existence.

Size.—This is a comparatively small species. The usual size is under 10 inches. The largest specimen known at present is that recorded by Jordan and Swain from Cedar Keys, Fla., 39 cm. (15 inches).

Distinctive characters and relationship.—The great majority of specimens may be readily recognized by the distinctive color pattern, the presence of three very prominent spots, considerably more prominent than the other spots on the body. These three spots form the angles of an imaginary scalene triangle, the apex of which is on the lateral line about three-quarters of the distance from the gill opening to the base of the caudal fin, the other two angles being above and below the lateral line, on a somewhat oblique base falling a little behind the posterior angle of the curve in the lateral line. This distinctive color pattern is present in specimens as small as 17 mm. Individual fish are frequently found in which the color pattern is not saliently distinctive, the three spots are either fainter and hardly ocellated approaching thus to the color of *lethostigma*, or there are supernumerary ocellated spots posteriorly somewhat as in *dentatus*. Such individual fish may be distinguished by the fin ray, gill raker and scale counts. For a discussion of the proper placement of infrequent specimens at the border line see page 282.

Biology.—No special investigation of the biology of this species has ever been made, and consequently there is little data extant in regard to it. Hildebrand and Cable (1931: 469) report that "a few female *Paralichthys albiguttus* with large roe were seen in October and November." Young fish taken by J. C. Pearson on the coast of Texas, during 1927, measured as follows: February 23, Laguna Madre, 4 specimens, 41, 42, 45, and 47 mm.; March 16, Hog Island, 5 specimens, 17, 29, 33, 42, and 52 mm.; March 30, Corpus Christi Pass, 2 specimens, 18 and 61 mm. The spawning season is, therefore, probably in late fall or in winter. The data given by Hildebrand and Cable in regard to young *Paralichthys* at Beaufort, and discussed in this paper under *dentatus*, also include the present species. As in the other species of *Paralichthys* it evidently spawns offshore.

Economic importance.—This species is evidently of minor economic importance in the southern States, the common commercial flounder there being *lethostigma*. Most specimens over 15 inches in length that are obtained by spears are of the latter species. While the relative quantities of the two species in the catch are unknown at present, not being distinguished by the fishermen or dealers when selling flounders, the numbers of *albigutta* entering trade channels are not large. On a visit to the French Market in New Orleans, only one specimen of the present species, about 15 inches long, was observed, although the stalls were then abundantly supplied with *lethostigma*. An examination of the catch brought in by the giggers in Apalachicola, Fla., for several days in succession, revealed only one small specimen of *albigutta* which was thrown away; all the others being *lethostigma*.

Pseudorhombus ocellaris Jordan and Gilbert (in part), Proc. U. S. Nat. Mus. 1: 370, 1879 (Beaufort, N. C.).

Pseudorhombus dentatus Jordan and Gilbert (in part), ibid. (Beaufort, N. C.).—Goode and Bean (in part), ibid. 2: 123, 1879 (U.S.N.M. 4887 from Florida belongs to this species. In their accompanying table of measurements and counts this specimen bears the heading, "*albigutta* type").

Paralichthys albigutta Jordan and Gilbert, ibid. 5: 302, 1882 (Pensacola, Fla.; Beaufort, N. C.).—Jordan and Gilbert, Bull. U. S. Nat. Mus. 16: 823, 1883 (South

Atlantic and Gulf Coasts).—Jordan and Swain, Proc. U.S.N.M. 7: 233, 1884 (Cedar Keys, Fla.).—Jordan, ibid. 9: 29, 1886 (Beaufort, N. C.).—Jordan and Goss, Rept. U. S. Comm. Fish. 1886: 248, 1889 (South Atlantic and Gulf coasts of the United States).—Henshall, Bull. U. S. Fish. Comm. 9: 382, 1891 (Marco, Gordon's Pass, Big Gasparilla, and Lemon Bay, Fla.).—Lönnberg, Ofvers. Svensk. Vet. Akad. Forh. 51: 130, 1894 (Clearwater Harbor, Hillsborough Co., Fla.).

Paralichthys lethostigma Evermann and Bean (in part), Rept. U. S. Comm. Fish., 1896: 248, 1898 (specimens from Indian River at Fort Pierce only, according to Evermann and Kendall, 1900).

Paralichthys albiguttus Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3): 2631, 1898 (Cedar Keys, Fla.).—Evermann and Kendall, Rept. U. S. Comm. Fish., 1899: 96, 1900 (Key West).—Linton, Bull. U. S. Bur. Fish. 24: 411, 1905 (food and parasites of the species at Beaufort, N. C.; probably not well distinguished as to species).—Smith, Fish. North Carolina, p. 388, 1907 (Bird Shoal, Point Lookout, and Fort Macon, N. C.).—Kuntz, Bull. U. S. Bur. Fish. 35: 1–30, 1918 (histological basis of color changes).—Hildebrand and Carle (in part), Bull. U. S. Bur. Fish. 46: 464–476, fig. 86–87, 1930 (Beaufort, N. C.).—Norman, Monogr. Flatfishes, p. 75, fig. 41, 1934 (North Carolina; Cedar Key, Fla.; Apalachicola Bay, Fla.).

PARALICHTHYS VORAX

Diagnosis.—Scales cycloid on both sides, 48; modified scales in lateral line 24 in arch, 49 in straight part. (The single small specimen examined without accessory scales.) Gill rakers short, 4 + 12 (3 + 11 on eyed side). Anal rays 54; dorsal 75; pectoral 10 on both sides. Origin of dorsal over anterior margin of upper orbit. Maxillary reaching a vertical through posterior margin of lower orbit. Depth 42.7, head 31, maxillary 15.8, interorbital 2.2. Sinistral.

Color.—Dark, mottled with shades of greater or lesser intensity; spots not conspicuous, some very faintly suggesting ocelli, but no definite ocellated spots present; jaws and snout of blind side blackish, the dark pigmentation continued along upper and lower profiles, gradually becoming more diffuse posteriorly, except upper and lower margins of caudal peduncle black; cheek of blind side dusky.

Specimen examined and geographic distribution.—The above account is based on a single specimen, 103 mm., from Recife, Brazil, collected by Dr. R. von Ihering (102370). This is the only definite locality which may be stated at present. The type locality is given as South America without further designation. This species was probably confused by some authors with *brasiliensis* and consequently its geographical distribution still remains to be determined. It is possible that some of the references given under *brasiliensis* refer partly or wholly to this species.

Distinctive characters and relationship.—In the essential diagnostic structural characters this species agrees closely with *albigutta* from the coast of the United States. The number of fin rays and scales and the proportional measurements are very nearly the same in both species. An examination of numbers of specimens may possibly reveal differences in the frequency distributions of the number of gill rakers and pectoral rays, the single specimen studied having these counts at the upper and lower limits, respectively, of the frequency distributions as determined for *albigutta*. Specimens of *albigutta* of the same size as the one of *vorax* described above, already have accessory scales developed, whereas the present specimen shows no trace of such scales. This species does not have the ocellated spots characteristic of *albigutta*.

As compared with the known species of its subgenus occurring with it or near its geographical range, namely, *brasiliensis* and *tropicus*, this species may be readily distinguished by its larger scales. It further differs from *brasiliensis* in the smaller number of gill rakers. *P. vorax* evidently bears the same relation to *brasiliensis* as *albigutta* bears to *dentatus* on the east coast of the United States.

Rhombus aramaca Castelnau (not Cuvier), Anim. Nouv. Rar. Amer. Sud. Poiss., p. 18, pl. 40, fig. 3, 1855 (Bahia).

Pseudorhombus vorax Guenther, Cat. Fish. Brit. Mus. 4: 429, 1862 (South America).

Paralichthys brasiliensis Norman, Monogr. Flatfishes, p. 77, fig. 43, 1934 (based on types of *vorax*).

Paralichthys vorax Ginsburg, Jour. Washington Acad. Sci. 26: 132, 1936 nomenclature discussed).

PARALICHTHYS TROPICUS

(PLATE 14)

Diagnosis.—Scales cycloid on both sides; 67. Accessory scales present on both sides, numerous, except in an area along middle posterior part of body; most other scales on body having a complete circle of small accessory scales around their edges. Gill rakers rather short, 11 on lower limb (12 on eyed side of the single specimen studied) of first gill arch, 2 on upper limb at the angle with two tuberosities above. Anal rays 58; dorsal 75;

pectoral 11. Vertebrae 10+26. Origin of dorsal nearly over anterior margin of eye. Maxillary reaching slightly past a vertical through posterior margin of orbit. Depth 43.9, maxillary 13.6, head 28.1, interorbital 2.2. Sinistral. The single known specimen is now faded, and color pattern of the species is unknown.

Specimen examined.—The foregoing account is based on the type, 321 mm. (34919), taken at lat. 10°37′40″ N., long. 61°42′40″ W. (off Trinidad, West Indies), in 31 fathoms.

Distinctive characters and relationship.—In the structural characters studied *tropicus* is apparently near to *vorax* from Brazil differing in having smaller scales. Although only one specimen of each species was examined, the difference in the scale count (table 1) is so pronounced that there is hardly any question that they belong to distinct species. Other differences between the two species remain to be determined. Very likely *tropicus* will prove to have a more profuse development of accessory scales.

Two other apparent near relatives of this species are *lethostigma* and *squamilentus* from the east coast of the United States. It apparently differs from both in having fewer vertebrae, and possibly also in having the accessory scales more profuse. It differs further from *lethostigma* in having fewer rays in the vertical fins, the counts of the type of *tropicus* falling decidedly out of the frequency distribution based on approximately 150 specimens of the other species (tables 5 and 6). It probably differs from *squamilentus* also in having fewer rays on the average; but judging by the few specimens examined, it is evident that these two species will be found to overlap, possibly rather widely, in this respect. The interorbital is appreciably narrower and the maxillary somewhat shorter than in *lethostigma*. The depth is less than in *squamilentus*. Although the precise degree of divergence between *tropicus* and these other two species remains to be learned by a determination of the range of variability of the distinguishing characters, there seems hardly any question that the single type specimen belongs to a distinct species.

It is apparently more remotely related to *brasiliensis*, a common species of its subgenus occurring nearer its range, differing chiefly in the number of gill rakers on the first arch and the number of vertebrae; *tropicus* having a total of 13 gill rakers and 10+26 vertebrae, while the corresponding counts in *brasiliensis* are 18 to 22 and 11+23, respectively.

Paralichthys tropicus Ginsburg, Proc. U. S. Nat. Mus. 82 (20) : 4, 1933 (off Trinidad, West Indies).

PARALICHTHYS LETHOSTIGMA

Southern large flounder

(PLATE 15)

Common name.—This species is generally called "flounder" without any qualifying word to distinguish it from other flounders. Some fishermen distinguish it by the term "mud flounder" p. 324). Since, however, this is the only commercial flounder of value on the coast of the Southern States that designation is not deemed appropriate and the term "southern large flounder" is suggested as a uniform common name for the species to distinguish it from other flounders.

Diagnosis.—Scales cycloid on both sides at all ages; 52 to 74, nearly all individuals falling in the range between 56 and 67, the mode at 60. Accessory scales rather sparse, sometimes numerous in large specimens (although not quite so many as in *dentatus*, or *albigutta*), usually beginning to appear in specimens 110 to 120 mm. in length, sometimes very few present in much larger fish. Total number of gill rakers on first arch ranging 10 to 13, nearly all having 11 or 12 (these two numbers occurring with approximately equal frequency); nearly always 2 on upper limb, infrequently 3; 8 to 11 on lower limb, nearly all specimens having 9 or 10. Anal rays 63 to 73, the mode at 69 (77 in one specimen); dorsal 80 to 95. Pectoral rays 12 in the majority of fish, frequently 11, sometimes 13 (12 on both sides in 6; 11 on both sides in 2; 12 on eyed side and 11 on the other in 2; 13 on eyed side and 12 on the other in 1; 9 on eyed side and 11 on blind side in 1, the last evidently being abnormal in this respect). Vertebrae 10 or 11+27 (in 2 specimens). Origin of dorsal usually somewhat in front of anterior margin of eye in large fish and somewhat behind anterior margin in specimens under 100 mm. Posterior extremity of maxillary reaching to a vertical through posterior margin of pupil in specimens of about 35 mm., through posterior margin of eye at about 50 to 100 mm., past eye in specimens over 100 mm. Interorbital rather wide, becoming markedly broad in large fish, conspicuously more

so than in related species. Body becoming deep in large individuals. Sinistral.

Color.—Body irregularly shaded with darker and lighter. The five longitudinal rows of spots more or less evident, usually diffuse, blending more or less with the darker shadings, and tending to disappear entirely in large individuals. None of the spots ocellated. Sometimes the spots are saliently distinct in specimens up to about 150 mm., and in such individuals the three spots forming the large triangle are most prominent as in *albigutta*, but they are not ocellated. The relative intensity of the shadings on the body is subject to great variation as in related species; some specimens being very light all over, especially in life, and others being very dark. After being landed, specimens of this species usually have whitish spots irregularly snowed over the body; these usually disappear after the death of the fish, but are sometimes present also in preserved specimens.

Small fish, between 20 and 45 mm., show characteristic groups of chromatophores, each group consisting of a blotch-like concentration of minute pigment dots interspersed with coarser chromatophores. This grouped concentration of chromatophores gives a gross appearance of blotches which may be somewhat coalescent. The coarser chromatophores may be also scattered between the blotches, but they are especially concentrated on them. The characteristic appearance of these groups is well shown in Hildebrand and Cable's figure 88, although in most specimens they are not so saliently prominent. One group on the midline, about two-thirds of the distance from the gill opening to the base of the caudal and two others near the angle of the curve in the lateral line, one above and one below, tend to be most prominent. The three most prominent groups are in the same position as the three ocellated spots in *albigutta*, that is they form the characteristic large triangle of related species, but these spots in the young of *lethostigma* are not ocellated. The young of *lethostigma*, of about 20 to 40 mm., have the color pattern very similar to those of *dentatus* of the same size; but after the material is properly separated some small differences become apparent which are typical of *lethostigma*. The two spots at the posterior ends of the subdorsal and supra-anal rows are not as prominent as in *dentatus;* the coarse chromatophores that overlay the dark blotches in groups, are characteristically more numerous in *lethostigma;* the other blotches on the body, in addition to the three most prominent ones, are usually more distinct than in *dentatus*. In *lethostigma* the other blotches are sometimes of nearly equal intensity as the three forming the large triangle.

In still smaller individuals, 13 to 20 mm., the groups of chromatophores are more diffuse and so arranged that they sometimes suggest broad cross bands. At about that size, specimens of *albigutta* resemble somewhat those of *lethostigma*. Specimens of 50 mm. or over generally have the color pattern of large fish.

Specimens examined.—Edenton, Albermarle Sound (collected by B. Schwartz): Avoca (23103); Beaufort (51898; also, many specimens from collection of U. S. Bur. Fish. Biological Station) and Cape Fear River (25591): N. C. Charleston, S. C. (17119 and 17120). St. Simons Sound, Ga. (collected by W. W. Anderson). St. Johns River (21279, the lectotype) and Apalachicola Bay (collected by E. Danglade and by me), Fla. Mississippi (8026). Biloxi Bay, Miss. (collected by Stewart Springer). Off Breton Island (collected by Stewart Springer): Bay Adams, off Grand Terre, Barataria Bay, Bay des Ilettes, Bayou Rigaud, Bayou Fifi, off Grand Isle, Caminada Bay and Callou Bay (collected by me): La. Galveston (31028 and 73590); Matagorda Bay (63652); Indianola (9388); Mission Bay, Mud I., Hog I., Oso Bay, Aransas Pass, Harbor I. and Corpus Christi Pass (collected by John C. Pearson); Tex. Specimens studied in detail 159; about 100 more examined to check one or another of the important characters; size of those examined ranging from 13 to 659 mm.

Geographic distribution and habitat.—The range of the specimens studied extends from Edenton, Albemarle Sound, N. C., to Corpus Christi Pass, Tex. This also represents the range of the records in the literature, which are based on specimens undoubtedly belonging to the present species. Extant records in the literature north of Albemarle Sound are evidently in error as pointed out later. It yet remains to be discovered whether the species is continuous in its range around the tip of the peninsula of Florida. The southernmost records of the species now extant are, Indian River on the east coast and Tampa Bay on the

west coast of Florida. It is common or abundant throughout its range.

This species has been recorded a number of times as occurring north of Albemarle Sound. Smith (1907) states that "It ranges as far north as New York, but is most common from Chesapeake Bay to the Gulf Coast." From New York it has been recorded by Jordan and Goss (1889), by Jordan and Evermann (1898) and by Bean (6th Ann. Rept. Forest Fish Game Commission, New York, p. 472, 1902; ibid., 7th Ann. Rep., p. 456, 1903; Cat. Fish New York, p. 720, 1903).

Smith does not state whether he actually examined specimens from Chesapeake Bay; while, on the other hand, the rather extensive collections of *Paralichthys* made by Schroeder in Chesapeake Bay and reported on by Hildebrand and Schroeder (Bull. U. S. Bur. Fish., vol. 43, pt. 1, p. 165, 1928) all represented *dentatus* and not a single specimen of *lethostigma* was taken. In this study also, no *lethostigma* was found among the extensive collections obtained by others in Chesapeake Bay. It is, therefore, safe to state that the species does not occur in Chesapeake Bay.

Likewise, the repeated records of this species from New York evidently are not based on the study of any specimens collected there. They have a common origin and may be traced to an erroneous interpretation of De Kay's work (Zool. New York, Fishes, pp. 299–300) by Gunther (Cat. Fish. Brit. Mus., vol. 4, pp. 426–430, 1862) and Jordan and Goss (1889). De Kay described two species of left-handed-flounders which he designated as *Platessa oblonga* and *Platessa ocellifer*. Both of these species are evidently referable to *Paralichthys dentatus* (Linnaeus), judging by De Kay's accounts. His *Platessa ocellifer* is without a doubt the same as *Paralichthys dentatus*, since his figure shows the typical color pattern of that species, while no other species is known from New York to which this figure may apply. It, therefore, only remains to consider what his *oblonga* represents. The author distinguishes his *oblonga* from his *ocellifer*, by the angulated shape of the caudal, the lesser number of rays in the dorsal and the lack of ocellated spots. These three characters, as distinguished by De Kay, are not tenable. The number of dorsal rays as given by De Kay, 88 and 95, fall within the range of variation of *dentatus* (table 6, p. 279). The lack of ocellated spots in De Kay's *oblonga* may well be ascribed to his having dark individuals in which the ocellated spots are faint; such individual specimens of *dentatus* occur sometimes. *P. dentatus* always has an angulated caudal, and the material on which De Kay based his *ocellifer* with a supposedly rounded caudal, either had the caudal frayed at the end or it was shrunken so that it appeared rounded. There is hardly a doubt that *ocellifer* and *oblonga* of De Kay refer to the same species, *dentatus* of Linnaeus. This was correctly pointed out long ago by Storer (1846 and 1863).

Besides the three characters pointed out by De Kay, his figure shows another difference which, however, is not mentioned in the description, namely, that his *oblonga* shows a much wider interorbital. Gunther who did not have any specimens but relied solely on De Kay's account, kept the two species separate, emphasizing the differences in the interorbital width shown by the figures. Jordan and Goss following Gunther, also state that *ocellifer* and *oblonga* of De Kay are distinct and that the latter species is the same as *lethostigma*. This is evidently the basis of the frequent reference of *lethostigma* to New York. While the combination of wide interorbital and the lack of ocellated spots generally does distinguish *lethostigma* from *dentatus* when specimens of like size are compared, the former character varies greatly with size in both species and the latter varies much with individual fish. The decisive difference, the character which would show without a doubt whether the *oblonga* of De Kay was based on specimens of *lethostigma*, namely, the number of gill rakers, is not given by that author. Furthermore, De Kay states in regard to his *oblonga* that it "is common along our sandy shores, and is procured abundantly in the months of September and October." This statement certainly can not apply to *lethostigma*. On the basis of the data now extant, therefore, the present species is not known to occur north of North Carolina.

The species prefers a mud bottom (p. 324), and is generally found along the shore, in bays, sounds and lagoons in comparatively shallow water where it is captured readily by spearing. This flounder also enters fresh water where it is sometimes taken in numbers. It has been reported from Lake George, St. John's River, and Ocklawaha River

in Florida (Goode 1884) and from Roanoke River in North Carolina (Smith 1893 and 1907). Specimens from Edenton and from Avoca, on Chowan River, N. C., were examined by me. I was told by fishermen that it is taken by spears along the banks of the Mississippi for considerable distances above the mouth.

Size.—This is the largest flounder on the coast of the Southern States. Fish brought to the market by giggers are usually between 12 and 20 inches. The largest examined is an individual 26 inches (660 mm.), including the caudal fin, from Beaufort, N. C. Jordan and Gilbert (1883, p. 617) report a maximum length of 30 inches at Charleston, S. C. However, in view of the paucity of records, it is quite possible that the species attains a considerably larger size.

Distinctive characters and relationship.—On the Gulf coast and the east coast of Florida where *albigutta* is common, this species may be readily distinguished, as a rule, by its distinctive color, all of the spots being diffuse, none especially prominent and not definitely ocellated. Doubtful specimens are separable by the combination of higher fin ray and scale counts (tables 1, 5, and 6). In the northern part of its range, North Carolina to northern Florida, where *dentatus* also occurs, *lethostigma* may be distinguished from that species by the lack of ocellated spots, and more especially by the fewer gill rakers there being no intergrading individuals with respect to this character, as between these two species. A count of the gill rakers on the first arch will positively distinguish *lethostigma* and *dentatus* in every case (tables 2 to 4). From the deep water *squamilentus*, this species may be distinguished by the depth of the body aided by the fewer gill rakers and other characters (p. 334). *P. lethostigma* also has a wider interorbital than the other three species, except in the small specimens.

Neotype.—Jordan and Gilbert in 1883 gave a recognizable description of this species under the name of *P. dentatus;* but the given synonymy and distribution do not apply altogether to it. Later, in 1885, they establish the name *lethostigma* based solely on their account of 1883. Since that account is based on more than one species it is necessary to fix definitely the status of *lethostigma* by the selection of a type. Jordan and Gilbert's account of 1883 does not contain any statements by which any of the specimens forming the basis of their description may be identified now. In their synonymy they cite Goode and Bean 1879, and the latter authors give museum numbers of the specimens examined by them. One of those specimens, 21279, from Indian River, Fla., 292 mm., is herewith designated as a neotype.

Biology.—No special study was ever made of this species and consequently very little is known regarding its habits and life history. Spawning probably takes place in late fall and early winter and the spawning season is possibly extended. John C. Pearson, in connection with his studies of the life history of the sciaenids on the coast of Texas obtained some young of this species as follows: In 1926, March 31, Corpus Christi Pass, 1 specimen 53 mm. In 1927, January 25, Harbor I., 3 specimens, 23, 24, and 31 mm.; February 15, Mud I., 4 specimens, 27, 28, 31 and 47 mm.; Feb. 23, Laguna Madre, 5 specimens 33, 36, 59, 62 and 65 mm.; March 11, Laguna Madre, 2 specimens 77 and 89 mm.; March 30, Corpus Christi Pass, 3 specimens, 89, 111, and 114 mm. These few individuals perhaps indicate that the spawning season is in late fall, and they show a fairly rapid growth to the end of March.

Fishery and economic importance.—A comparatively important fishery for this species exists on the coast of the Southern States from North Carolina to Texas. The most important method in commercial fishing is by means of spears, the operation being known as "gigging," "flounder-lighting" or "floundering." The fishermen's outfit is simple. Besides the spear or "gig," it consists of a flat-bottomed skiff having an iron rod attached to the stern in a nearly but not quite upright position and a wire basket suspended from the upper end of the rod. A flaring fire is lit in the basket by burning pine-knots, called "fatwood." The skiff is poled along in the shallows, and as the bright flame divulges the position of a flounder it is speared. Fishing may be carried out by two men, one poling and the other spearing the fish; but often one man does all the work. Gigging is usually done on dark, calm nights, at the incoming tide with which the fish come into shallow water. On bright moonlight nights or when a wind is blowing, gigging is said not to yield very satisfactory results.

Besides gigging, a method of capture employed in the Southern States for taking flounders especially, this species is taken in considerable quantities in haul seines, trammel nets, gill nets, and, to a lesser extent, in shrimp trawls. The flounders taken with these types of gear are mostly obtained incidentally, while fishing for other species, or in general fishing operations.

The annual yield of this species, in round figures, is 3,232,000 pounds worth $440,000 to the fisherman. These figures are obtained from the published statistics of the Fish and Wildlife Service under the heading of "flounder" from North Carolina to Texas for the year 1945. The "flounder" catch of the Southern States consists chiefly of *Paralichthys lethostigma* with a small admixture of *Paralichthys albigutta*, except that the catch in North Carolina, consisting of 1,203,000 pounds, includes a considerable and unknown percentage of *Paralichthys dentatus*.

Racial differentiation.—The number of gill rakers in the population of *lethostigma* on the Atlantic coast apparently averages higher than that on the Gulf coast as shown below. Of the 6 specimens having 11 gill rakers on the lower limb, 5 came from North Carolina and Georgia and only 1 from Louisiana; although this character was determined in only 23 specimens from the Atlantic coast as compared with 121 specimens from the Gulf coast. All specimens having 8 gill rakers came from the Gulf coast. The modes apparently are at 9 and 10 on the Gulf and Atlantic coasts, respectively.

	Gill rakers on lower limb			
Number	8	9	10	11
North Carolina to Georgia frequencies		7	11	5
Louisiana and Texas frequencies	7	60	53	1

Chaenopsetta dentata Gill (not Linnaeus), Proc. Acad. Nat. Sci. Philadelphia, 1864: 218 (Charleston, S. C.).

Lophopsetta maculata Yarrow, ibid., 1877: 205 (Beaufort, N. C.: judging by size recorded and by description of fishery probably relates to present species possibly including also *dentatus*).

Pseudorhombus oculiaris Jordan and Gilbert (in part), Proc. U. S. Nat. Mus. 1: 370, 1879 (Beaufort, N. C.; according to Jordan, 1886).

Pseudorhombus dentatus Jordan and Gilbert (in part), ibid. (North Carolina).—Goode, ibid., 2: 110, 1879 (St. Johns River and St. Augustine, Fla.).—Goode and Bean (in part), ibid., p. 123, 1879 (South Carolina; Florida; Texas).—Bean (in part), ibid., 3: 79, 1880.

Paralichthys dentatus Jordan and Gilbert, Proc. U. S. Nat. Mus. 5: 302, 1882 (Pensacola, Fla.; Galveston, Texas; New Orleans, La.).—Jordan and Gilbert, ibid., p. 617, 1883 (Charleston, S. C.).—Jordan and Gilbert, Bull. U. S. Nat. Mus. 16: 822, 1883 (description only refers to this species not the synonymy nor distribution).—Bean, ibid., 27: 431, 1884 (Galveston, Tex.).—Goode (in part), Fish. Ind. U. S. Sec. 1, p. 179, pl. 42, 1884 (figure and part of account refer to this species).

Paralichthys lethostigma Jordan and Gilbert, Proc. U. S. Nat. Mus. 7: 237, 1884 (species established on description of Jordan and Gilbert 1883, p. 822; no type specimen indicated).—Jordan, ibid., 9: 29, 1886 (Beaufort, N. C.).—Jordan and Goss, Rept. U. S. Comm. Fish., 1886: 247, pl. 3, fig. 7, 1889 (part of synonymy and distribution in error).—Smith, Bull. U. S. Fish. Comm. 11: 196 and 200, 1893 (Edenton Bay and Roanoke River at Plymouth, N. C.).—Evermann and Kendall, ibid., 12: 119, 1894 (Galveston, Dickinson Bayou and Corpus Christi, Tex.).—Henshall, ibid., 14: 220, 1895 (Tampa, Fla.).—Evermann and Bean (in part, Rept. U. S. Comm. Fish., 1896: 248, 1898 (specimens from Indian River at Stuart only, according to Evermann and Kendall 1900).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3): 2630, 1898 (part of synonymy and distribution in error).—Evermann and Kendall, Rept. U. S. Comm. Fish. 1899: 96, 1900 (Tampa Bay, Fla.).

Paralichthys dentatus Fowler (in part), Ann. Rept. New Jersey State Mus., 1905: pl. 87, 1906 (the figure evidently a copy of Goode (1884) from a specimen of this species, not the description).

Paralichthys lethostigmus Smith, Fish. N. C., p. 388, 1907 (Avoca, Albemarle Sound and Roanoke River at Plymouth, N. C.).

Paralichthys albigutius Hildebrand and Cable (in part), Bull. U. S. Bur. Fish. 46: 473–474, figs. 88 and 89, 1930 (Beaufort, N. C.; fin rays correctly indicated on the figures, also part of account applies to this species).

Paralichthys lethostigma Norman (in part), Monogr. Flatfishes, p. 74, fig. 40, 1934 (North Carolina; Charleston Harbor, S. C.; Florida; Biloxi Bay to Horn I., Miss.; the specimen recorded from Beaufort is an *albigutta*, that from Tobago probably a *tropicus*).—Ginsburg, Jour. Washington Acad. Sci. 26: 133, 1936 (general notes).

PARALICHTHYS SQUAMILENTUS
Broad flounder

Common name.—This flounder is a deep water species, living out of reach of the usual fishery operations for flounders hitherto pursued in the Gulf. For this reason it is largely unknown to the fishermen and failed to receive a popular name. The above name is suggested as appropriate as a uniform common name for the species, referring to its deep body.

Diagnosis.—Scales cycloid on both sides, 67 to 80. Accessory scales in sparse numbers, appearing late in life. Total number of gill rakers on first arch usually 14 or 15, varying 13 to 16; upper limb

usually with 3 or 4 gill rakers, sometimes 5; lower limb with 10 to 12. Anal rays 59 to 64; dorsal rays 76 to 83. Pectoral rays usually 12, frequently 11 (12 on both sides in 8 fish; 11 on both sides in 2; 11 on blind side and 12 on eyed side in 3; 12 on blind side 11 on eyed side in 1). Vertebrae 10+28 (in 1 specimen). Origin of dorsal over anterior margin of pupil at 30 mm., over space between anterior margin of eye and that of pupil in specimens 36 to 45 mm., over anterior margin of eye, varying slightly both ways, in specimens 96 to 370 mm. Maxillary reaching posteriorly to a vertical through hind margin of pupil in specimens 30 to 45 mm., through posterior margin of eye or nearly there in fish 96 to 370 mm. Body conspicuously deep. Sinistral.

Accessory scales.—Twelve specimens 30–120 mm., and one specimen 333 mm. virtually have no accessory scales. After prolonged search with a magnifier one such scale was found on one specimen each of 118 and 333 mm. Three specimens 342–370 mm. have accessory scales, but they are few in number and rather widely spaced. Evidently in this species the accessory scales develop late in life and they are few in number. In this character then, *squamilentus* approaches the genus *Pseudorhombus*.

Color.—Small specimens, 30 to 36 mm., with five longitudinal rows of spots as described above in the discussion of the generalized color pattern (p. 277), fairly well outlined, not ocellated; body characteristically sprinkled with pigment specks, somewhat like the published figure of the type specimen, suggesting a "fly specky" appearance, the specks nearly confined to a broad area along dorsal and ventral profile, area along middle of body virtually devoid of specks; a specimen of 333 mm. faintly showing non-ocellated spots in the subdorsal and supra-anal rows, one of 370 mm. without a trace of spots (other available specimens faded); both large specimens having the specks more numerous and crowded than the small specimens, and the blind side moderately dusky.

As compared with specimens of similar size, the small specimens of *squamilentus* examined differ from *lethostigma* and *dentatus* in not having the well marked groups of chromatophores characteristic of those two species, and from *albigutta* in the spots not being ocellated.

Specimens examined.—Pensacola, Fla., one specimen 120 mm., the type (30862); 1 specimen 100 mm. (30762); 5 specimens 96 to 118 mm. (32585). Corpus Christi Pass, Tex.; collected by John C. Pearson: 3 specimens 30 to 36 mm., March 23, 1927 (152881); 2 specimens 39 and 45 mm., March 30, 1927 (152882). Off Santa Rosa Island, Fla.; 105 fathoms; Stewart Springer; 2 specimens 333–370 mm. (152883). Tortugas, Fla.; 39 fathoms; W. H. Longley; 2 specimens 242 mm. (117069).

Geographic distribution and habitat.—Besides the localities listed above from which specimens were examined and the records by Norman and by Longley, this species has also been recorded from Egmont Key and Biscayne Bay, Fla., and Charleston, S. C., as noted in the bibliography. However, in view of the facts brought out by this investigation, the latter records need verification, although the species quite possibly does occur in those localities. The chief character by which *squamilentus* has been distinguished heretofore, was by the increased number of scales, but a study of table 1 shows that while this character is sufficient to distinguish this species from *albigutta*, the frequency distribution of the number of scales nearly falls within the range of *dentatus*, although averaging higher in *squamilentus*, and that it also intergrades with *lethostigma*. Especially the record from South Carolina possibly might have been based on a specimen of *dentatus* or of *lethostigma* having a high scale count. Although this specimen was supposed to have been deposited in the National Museum it was not found there during this investigation. The proper distinction of *squamilentus* depends on a combination of characters which must be studied in detail and with exactitude, since each character when taken by itself closely approaches or overlaps that of *dentatus* or *lethostigma*.

Specimens of this species are scarce in collections for the evident reason that it lives in deep water. Stewart Springer who preserved two of the large specimens forming the basis of this account states in a letter that "it apparently is abundant in 80 to 120 fathoms and could possibly turn out to be of commercial importance." The 5 small specimens examined from Corpus Christi were obtained inshore by John C. Pearson. It may be tentatively concluded then, that the young fish

live in shallow water and migrate in deep water to attain growth.

Size.—The largest specimen on record appears to be that by Longley, 415 mm., taken off Tortugas.

Distinctive characters and relationship.—This species is not easily separable from the three common east coast species. The number of dorsal and of anal rays overlaps that of *dentatus* or *lethostigma* and *albigutta*, respectively. The apex of the curve for *squamilentus* falls at the region where the extremities of the curves of the other three species overlap, being somewhat nearer to those of *albigutta*. To a lesser extent this is also true of the gill rakers. In the specimens counted there is no intergradation between *squamilentus* and *dentatus* with respect to the number on the lower limb, and a slight intergradation between this species and *lethostigma* with respect to the total number. However, more intergrades may well be expected when more specimens of *squamilentus* are examined. The scale count of *squamilentus* is markedly high; it does not intergrade with *albigutta;* intergrades with *lethostigma* and is massed at the upper extremity of distribution of *dentatus*. The body is notably deep. When all the characters are considered there should be no trouble in distinguishing *squamilentus*. It is separable from *albigutta* by the number of scales (table 1), aided—in case of specimens near the border line—by its depth and to a lesser extent by the other meristic characters and by color. Its separation from *dentatus* and *lethostigma* may be best accomplished by the depth, the variation in this character in *squamilentus* being fairly discontinuous in the specimens measured (table 8), as compared with the other two species. The depth character is greatly aided by the number of gill rakers, to a lesser extent by the number of fin rays and to some slight extent by the number of scales. The interorbital is not as wide as in *lethostigma*. The differences between *squamilentus* and *tropicus* are discussed on page 328. It differs from the other four species in having notably few accessory scales.

The general physiognomy of *squamilentus* is such that specimens usually may be identified at a glance. The 5 small fish from Corpus Christi Pass were distinguished by sight as being different than either *lethostigma* or *albigutta*, on a preliminary identification, before a detailed study of the specific characters was made, and not having any idea at the time what species they may represent. The features which chiefly draw attention to the present species are the deep body and the distinctive color. They show a certain characteristic "fly specky" appearance. It should be noted, however, that medium sized specimens of *albigutta* and large specimens of *lethostigma* are also rather deep-bodied and hardly separable from *squamilentus* on sight. The color also is not radically different than in the related species.

On account of its intermediacy in some important characters, the precise relationship of *squamilentus* is rather obscure. It is probably most nearly related to *lethostigma*.

Paralichthys squamilentus Jordan and Gilbert, Proc. U. S. Nat. Mus. 5: 303, 1882 (Pensacola, Fla.).—Jordan and Gilbert, Bull. U. S. Nat. Mus. 16: 823, 1883 (West Coast of Florida to South Carolina).—Bean, Bull. U. S. Nat. Mus. 27: 431, 1884 (Pensacola).—Jordan and Goss, Rept. U. S. Comm. Fish., 1886: 248, 1889 (South Atlantic and Gulf coasts of United States).—Henshall, Bull. U. S. Fish. Comm. 9: 382, 1891 (Egmont Key, Fla.).—McCormick, Rept. U. S. Comm. Fish., 1895: 176, 1896 (Biscayne Bay, Fla.).—Jordan and Evermann, Bull. U. S. Nat. Mus. 47 (3): 2631, pl. 374, fig. 923, 1898 (Pensacola, Fla.; Charleston, S. C.).—Norman, Monograph Flatfishes, p. 76, fig. 42, 1934 (Pensacola and Dry Tortugas, Fla.).—Longley, Carnegie Inst. Washington Pub. 535: 39, 1941 (Tortugas, Fla.; 45–110 fathoms).

SPECIES OF DOUBTFUL RELATIONSHIP

No specimens are available of the following species. Judging by extant accounts the generic affiliations of these species are somewhat doubtful; but their names were associated by authors with *Paralichthys*. They are treated here under the original names pending further research and a definite decision regarding their generic status.

PARALICHTHYS TRIOCELLATUS

The essential characters in the original author's account (1915) based on a specimen from Ilha Rasa, Brazil, are as follows: Scales largely ctenoid (not stated whether on one only or on both sides), 48. Accessory scales absent. Gill rakers 1 on upper limb, 8 on lower limb. A. 69, D. 86. Dorsal origin over anterior margin of eye. Interorbital much reduced. Head 28.5; depth 44.5; maxillary 2 in head. Prepeduncular spot present, ocellated; two other ocellated spots on a vertical about midway between base of caudal and posterior margin

of head, forming an isosceles triangle with the prepedunclular spot.

All the essential characters given by Miranda Ribeiro agree with those of *Pseudorhombus isosceles*, except that the body is not quite so deep as in that species. Norman examined four specimens in the British Museum, from Cape Frio, Brazil, which he thinks are identical with *triocellatus*. Norman's description is adequate to distinguish his specimens specifically from all known related flounders on the coast of Brazil and should his specimens prove to be conspecific with the type of *triocellatus*, the species is distinct from *isosceles*.

The essential characters in Norman's description of these four specimens are as follows: Scales mostly feebly etenoid on ocular side, cycloid on blind side; 40 ("about 60 in lateral line"). Very few accessory scales. Gill rakers 8 or 9 on lower limb. A. 67–69; D. 82–86. Dorsal origin in front of eye. Interorbital a narrow ridge. Teeth of moderate size, canines not much enlarged. Maxillary extending to a little beyond middle of eye, about 2 in head. Head 29–31; depth 40–43. Color same as above, except that prepedunclular spot sometimes lacking.

There are two important discrepancies in the accounts of the two authors. According to Miranda Ribeiro, *triocellatus* lacks accessory scales and the scale count is 48; while Norman's specimens have some accessory scales and the scale count is 40. These differences may possibly be due to individual variability, or to different methods of study followed by the two authors; but they may also indicate specific differences. A solution of these questions must wait until the range of variation of *triocellatus* is definitely established.

The interorbital in this species is reduced to a mere ridge, unlike that in any species of *Paralichthys*. Norman describes his specimens as having the teeth moderate which is also unlike that in most species of *Paralichthys*. Consequently, it is doubtful whether this species belongs to *Paralichthys*.

Paralichthys triocellatus Miranda Ribeiro, Bol. Soc. Agric. Rio de Janeiro 1904, p. 192 (citation not verified).—Miranda Ribeiro, Arch. Mus. Nac. Rio de Janeiro 17 (Heterosomata): 13, photo., 1915 (Ilha Rasa, Brazil).—Norman, Monogr. Flatfishes, p. 80, fig. 46, 1934 (Cape Frio, Brazil; 40 fath.).—Norman, Discovery Rept. 16: 135, 1937 (compared with *P. isosceles*).

PARALICHTHYS COERULEOSTICTA

This species was described from a single example 73 mm., from Juan Fernandez, Chile. The pertinent specific characters given in the original description are as follows: A slender spine at beginning of anal. Scales on eyed side thickly spinuliferous, esmooth on blind side; 50. Gill rakers on lower limb of first arch 20. A. 70; D. 87. Dorsal origin in front of eye. Eye 3 times in head. Interorbital very narrow. Teeth slender, pointed, gradually and not much increasing in length forward. Depth 45, head about 22, maxillary 7.3. Sinistral.

This species apparently shows characters of both *Paralichthys* and *Hippoglossina*, and if properly placed in the former largely destroys the boundary between those two genera. The dorsal origin is in front of the eye like *Paralichthys;* but the interorbital is narrow, the teeth are small and it has a preanal spine like *Hippoglossina*. Assuming it to be a *Hippoglossina*, it is to be noted further that the preanal spine, the short maxillary, the relatively many gill rakers and the rather large scales are like in the subgenus *Hippoglossina*, but the fin rays have a high count and the eye is medium large like in the subgenus *Lioglossina*.

On the basis of the original description it is not possible to place this species generically with confidence. It is very possible that it belongs to neither one of those two genera. This is further indicated by the unusually short head and maxillary, strikingly shorter than in any species of the two genera.

Paralichthys coeruleosticta Steindachner, Fauna Chilensis 1: 327 (Zool. Jahrbüch. supp. bd. 4) 1898 (Juan Fernandez I., Chile).—Delfin, Cat. Pec. Chile, p. 101, 1901 (listed).—Norman, Monogr. Flatfishes, p. 88, 1934 (after Steindachner).

HIPPOGLOSSUS KINGII

This name was based by Jenyns not on actual specimens, but on a drawing prepared by an officer of the *Beagle*. The figure published by Jenyns shows the following characters: Ventral short, with a short base, symmetrical. Interorbital wide, somewhat as in males of some species of *Syacium*, or in specimens of some other genera. A well

developed anterior curve in the lateral line. Scales large, in about 35 rows over straight part of lateral line. Pectoral short. Mouth rather large, maxillary extending approximately to under posterior margin of eye. Teeth comparatively large. Eye small. Body deep, sinistral. D. 66; A. 51; P. 11; ". . . fin-ray formula . . . computed from the recent fish." No spots or other distinctive color markings. Size unknown.

The figure further shows the first 18 dorsal rays subequal, rather abruptly lower than and separated from the succeeding rays, as though the dorsal was composed of two separate fins. This is unusual for a flounder, but not so far fetched as may appear. Some flounders now known from the coast of Chile, some species of *Paralichthys* for instance, have the anterior rays short, although the increase in length to the posterior rays is more gradual than represented in the figure. Assuming a tear in the interradial membrane in that position in the specimen from which the drawing was prepared, it may be readily conceived how this apparently misleading effect was produced by the artist.

It is impossible to determine with confidence the particular species of those now known from the coast of Chile, to which the original account may apply. Even its generic affiliation cannot be determined with assurance. The apparent best course to follow in this particular case would be to treat it as an unidentifiable species until the flounders from the coast of Chile are better known when it may possibly be placed with some measure of assurance.

The species was referred by later authors, generally with a query, to *Paralichthys* or *Pseudorhombus*, as shown in the bibliography. No author, except Fowler, assigned definite specimens to this species. Fowler described a specimen from the coast of Chile that he identifies with this species which he places in *Paralichthys*. The essential characters in his description, based on a mounted specimen, 740 mm., are as follows. Scales all cycloid, 80; A. 53; D. 66. Pectoral 12, "upper rays longest" . . . "large canines in lower jaw about equal each side; no upper canines and upper teeth best developed on blind side." Depth 43; head 28; maxillary 12, "reaches opposite front pupil edge." . . . "lower eye 10, 2 in interorbital". Sinistral.

Fowler's account also is inadequate to determine the genus to which his specimen belongs. Norman (Monogr., p. 84, 1934) suggests that Fowler's specimen may be a *Hippoglossina* on account of its comparatively few fin rays. However, it apparently has large teeth, a small eye and a wide interorbital, and consequently, can hardly belong to that genus. Also, the point at which the maxillary terminates is markedly more forward than in any species of *Paralichthys*, especially considering the large size of the specimen described, and it apparently does not belong to that genus either.

As compared with the figure published by Jenyns, the specimen described by Fowler apparently has smaller scales and a shorter maxillary. However, he is the first author to assign a definite specimen to *kingii*, and if no species which more nearly approaches Jenyns' figure is ever discovered on the coast of Chile, Fowler's restriction may be allowed to stand. But his specimen needs to be reexamined to definitely determine its status and generic affiliation.

Hippoglossus kingii Jenyns, Zool. Voy. Beagle, 4: 138, pl. 26, 1842 (Valparaiso).—Guichenot, in Hist. Fis. Pol. Chile, by Gay, Peces, p. 332, 1848.—Günther, Cat. Fish. Brit. Mus. 4: 423, 1862 (suggests that the species may possibly belong to Bleeker's genus *Pseudorhombus*).

Paralichthys adspersus Jordan and Goss, Rept. U. S. Comm. Fish. 1886: 246, 1889 (place under *adspersus* with a query).

Pseudorhombus kingii Reed, An. Univ. Chile 98: 665 (Cat. Pec. Chilenos, p. 16) 1897 (listed).

Paralichthys kingii Delfin, Cat. Pec. Chile, p. 104, 1900 (listed).—Fowler, Proc. Acad. Nat. Sci. Philadelphia 78: 282, 1926 (Chile).

Paralichthys adspersus Norman, Monogr. Flatfishes, p. 83, 1934 (placed in synonymy of *adspersus* with a query).

Paralichthys microps Norman, Disc. Rep. 16: 133, 1937 (placed in synonymy of *microps* with a query).

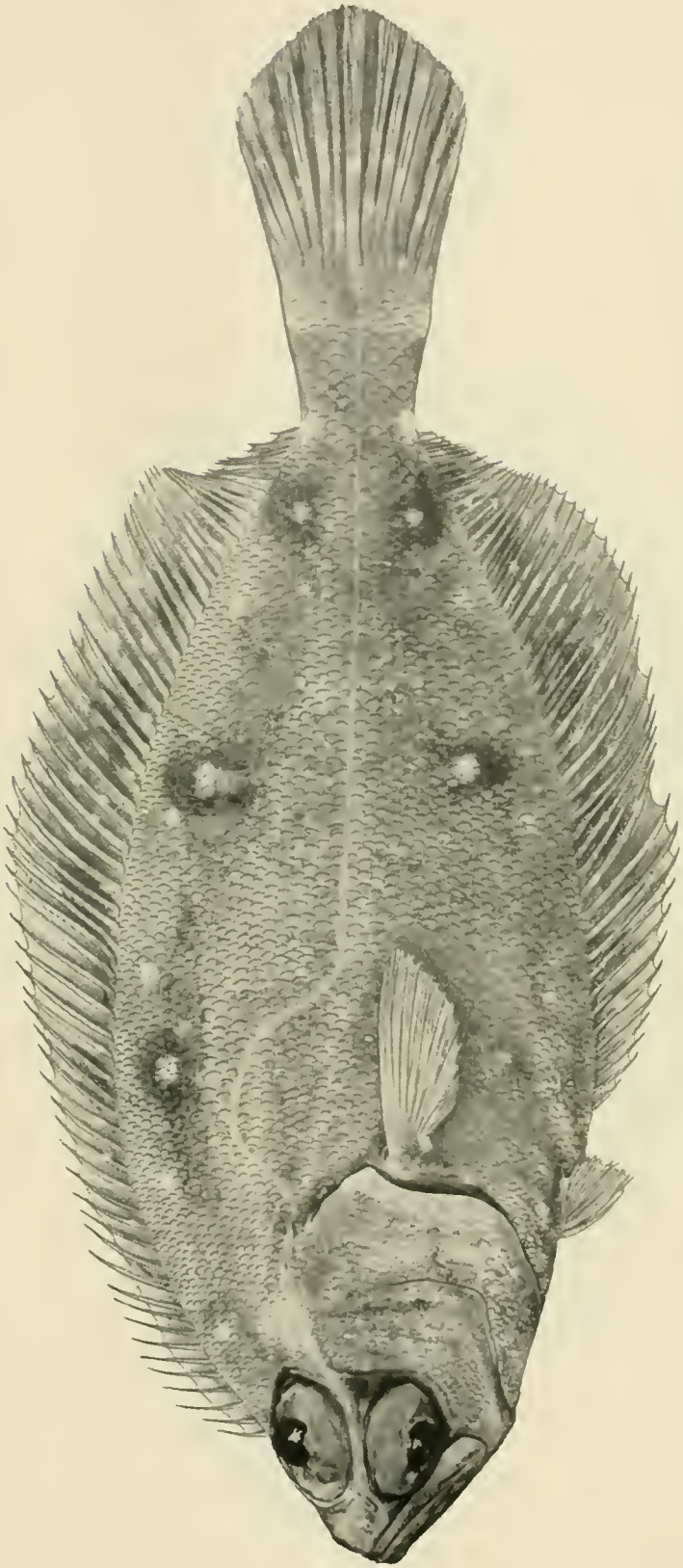

PLATE 1.—*Hippoglossina boltmani*, from a specimen 161 mm.; U. S. Nat. Mus. 111187; Panama Bay.

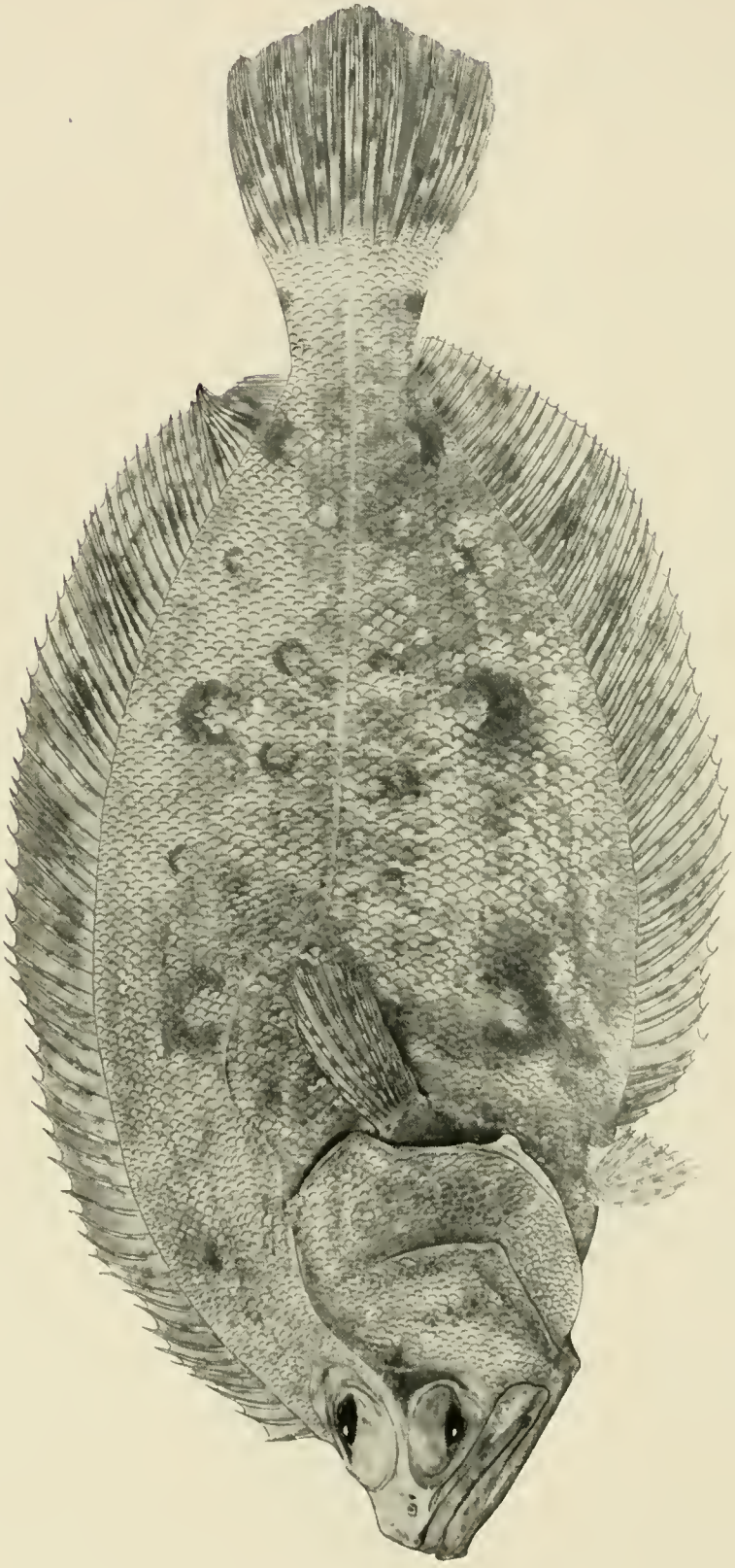

PLATE 2.—*Hippoglossina stomata*, from the lectotype, 315 mm.; U. S. Nat. Mus. 41905; San Diego, Calif., off Point Loma.

PLATE 3.—*Hippoglossina oblonga*, from a specimen 304 mm.; U. S. Nat. Mus. 33359, off Nantucket, Mass.

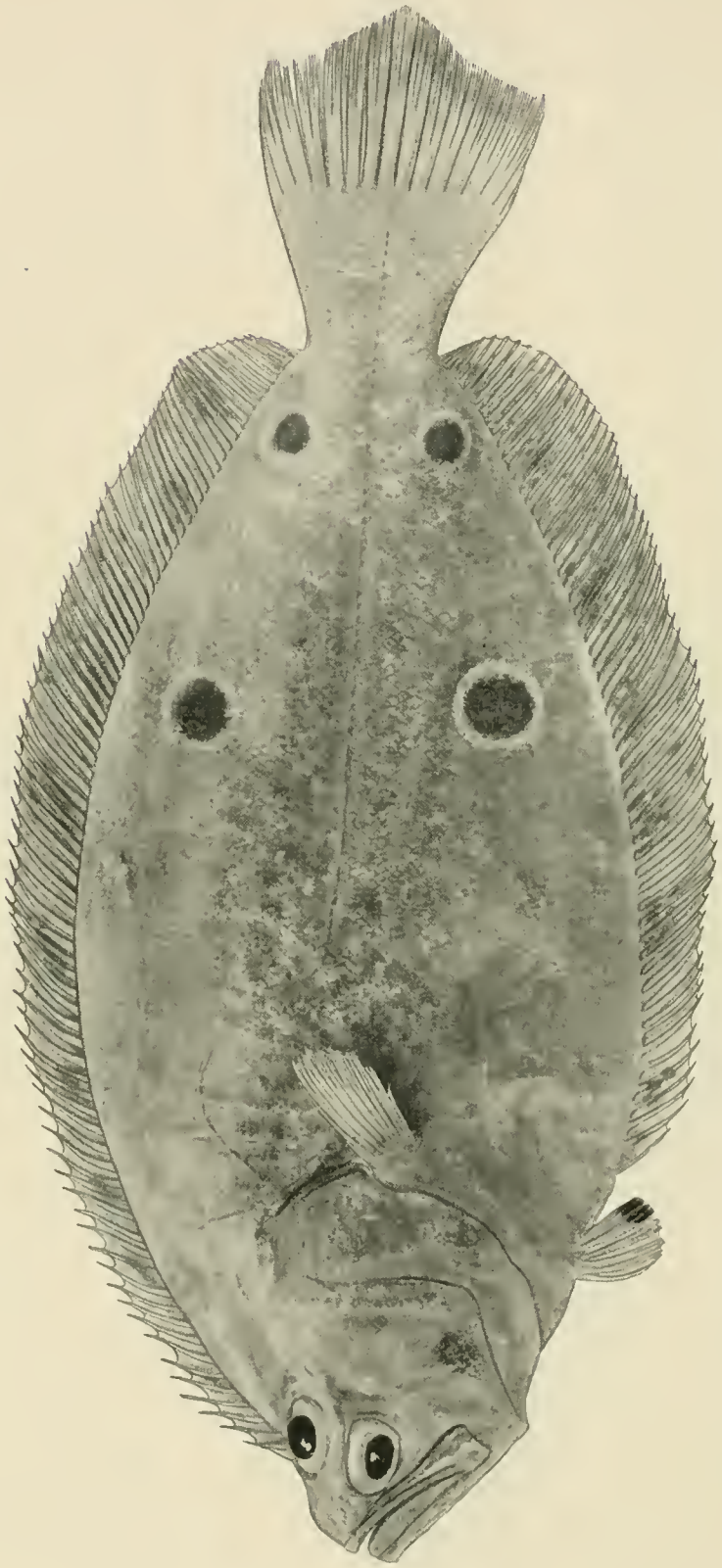

PLATE 4.—*Hippoglossina tetrophthalmus*, from the lectotype, 332 mm.; U. S. Nat. Mus. 17290; Gulf of California at Tiburon Island.

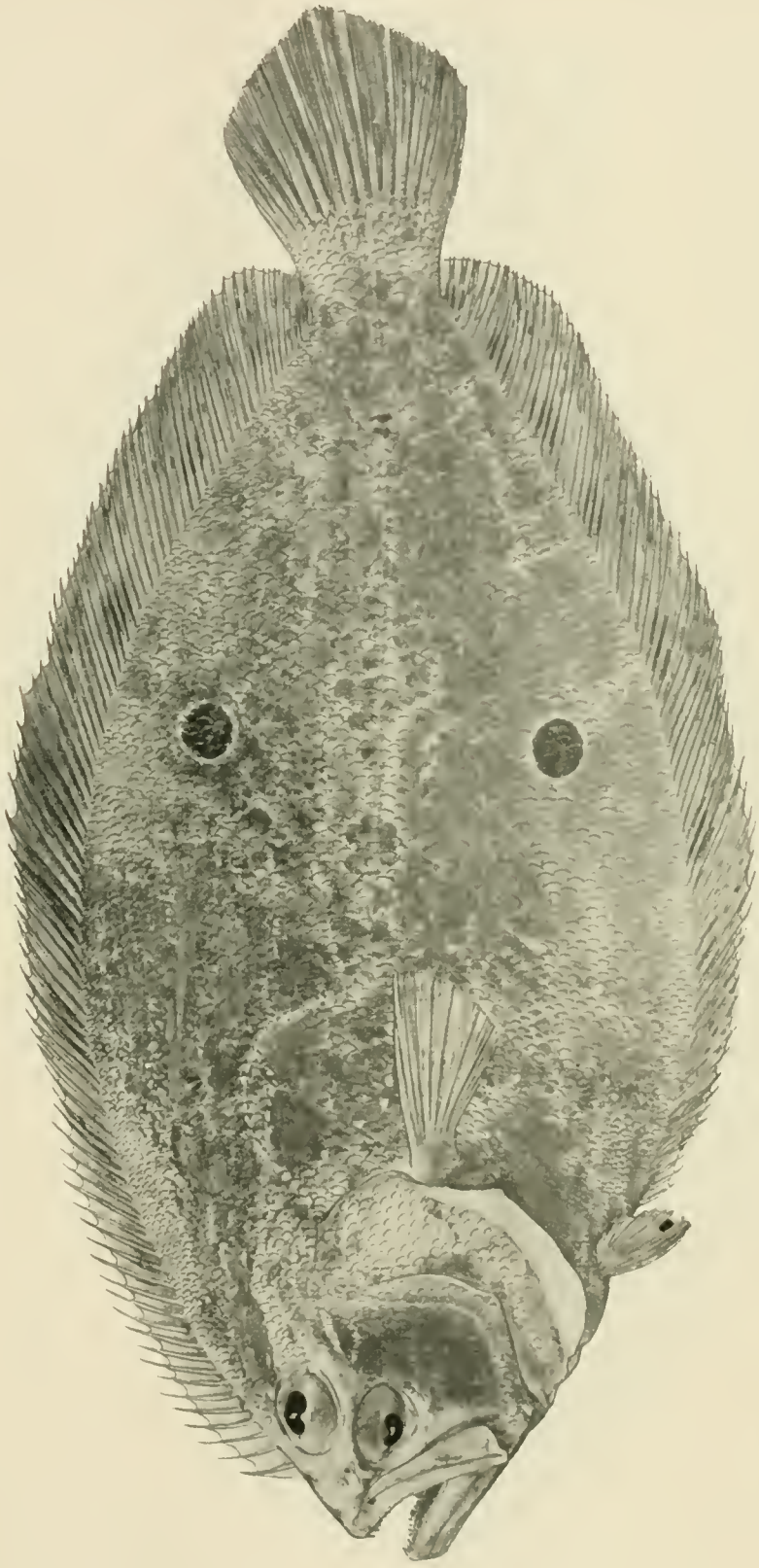

PLATE 5. — *Pseudorhombus isosceles*, from the lectotype, 217 mm., U. S. Nat. Mus. 43371; Bahia, Brazil; scales restored in large part; preopercular spot possibly partly faded in the three available specimens.

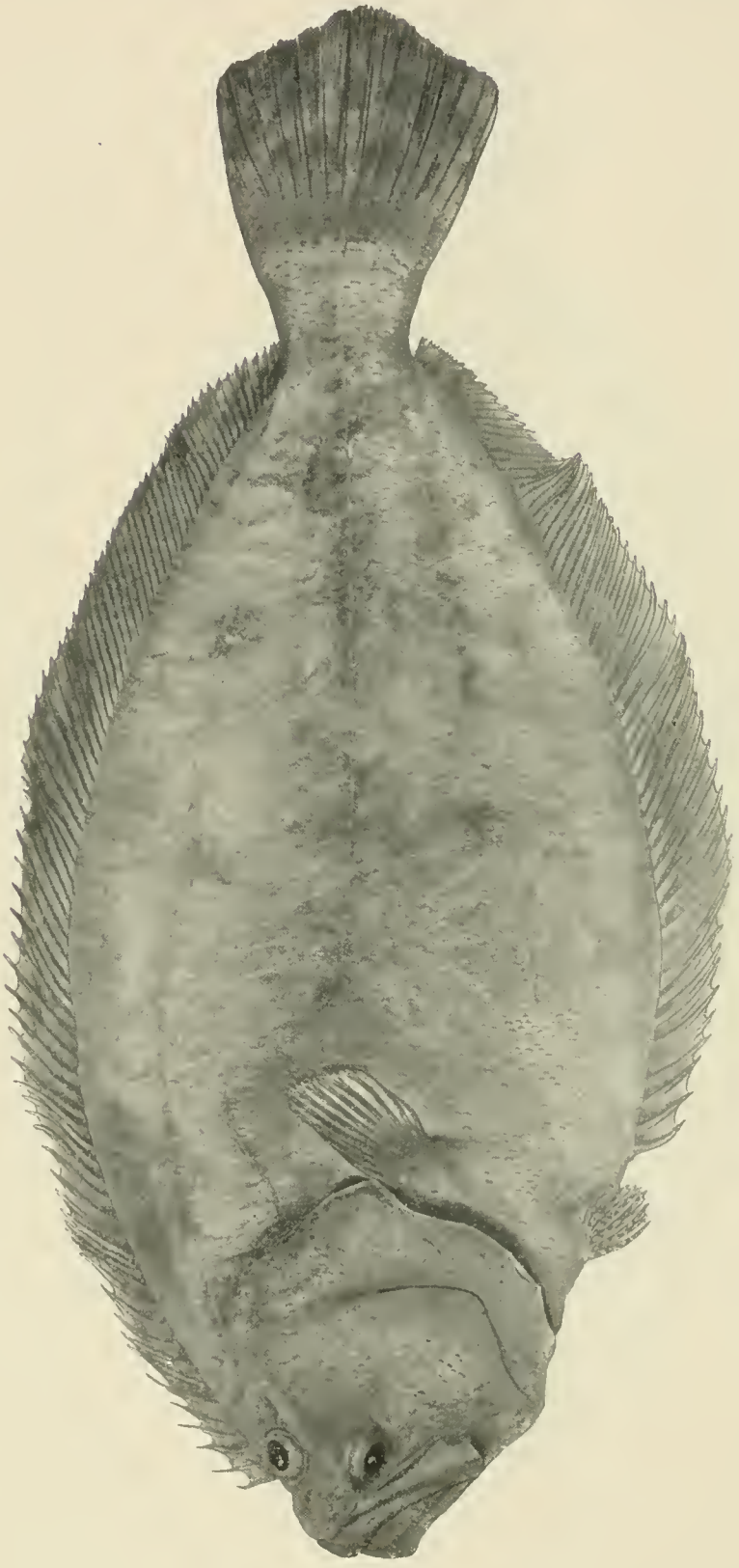

PLATE 6.—*Paralichthys schmitti*, from the type, 455 mm.; U. S. Nat. Mus. 88831: Juan Fernandez Island, Chile.

PLATE 7.—*Paralichthys schmidti*, blind side of same specimen as in plate 6, showing spots on fins and jaws.

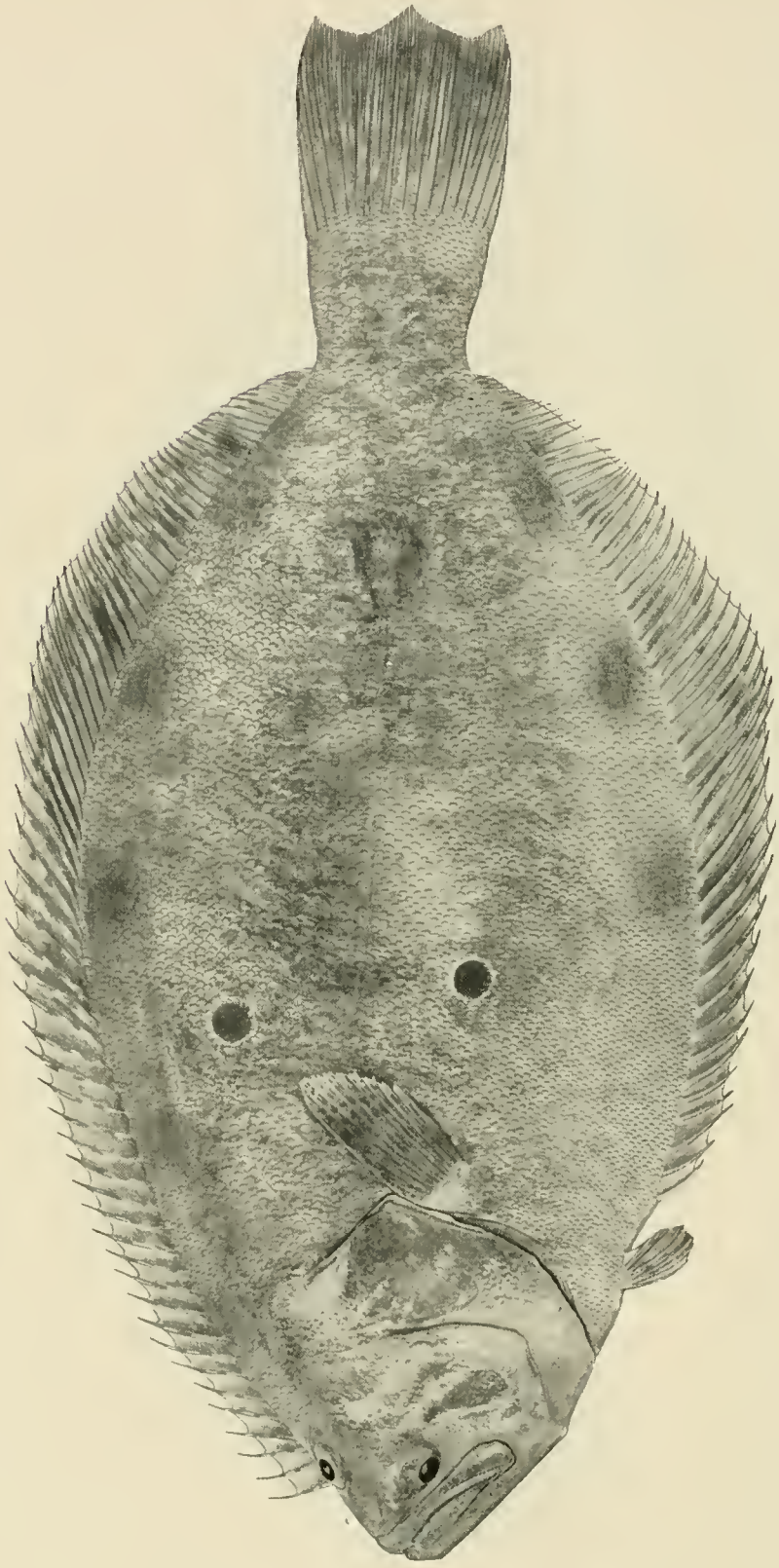

PLATE 8.—*Paralichthys adspersus*, from a specimen 388 mm.; U. S. Nat. Mus. 53490, Callao, Peru; the prepedunecular spot not plainly marked in the larger available specimens, possibly faded, well marked and ocellated in the smaller specimens.

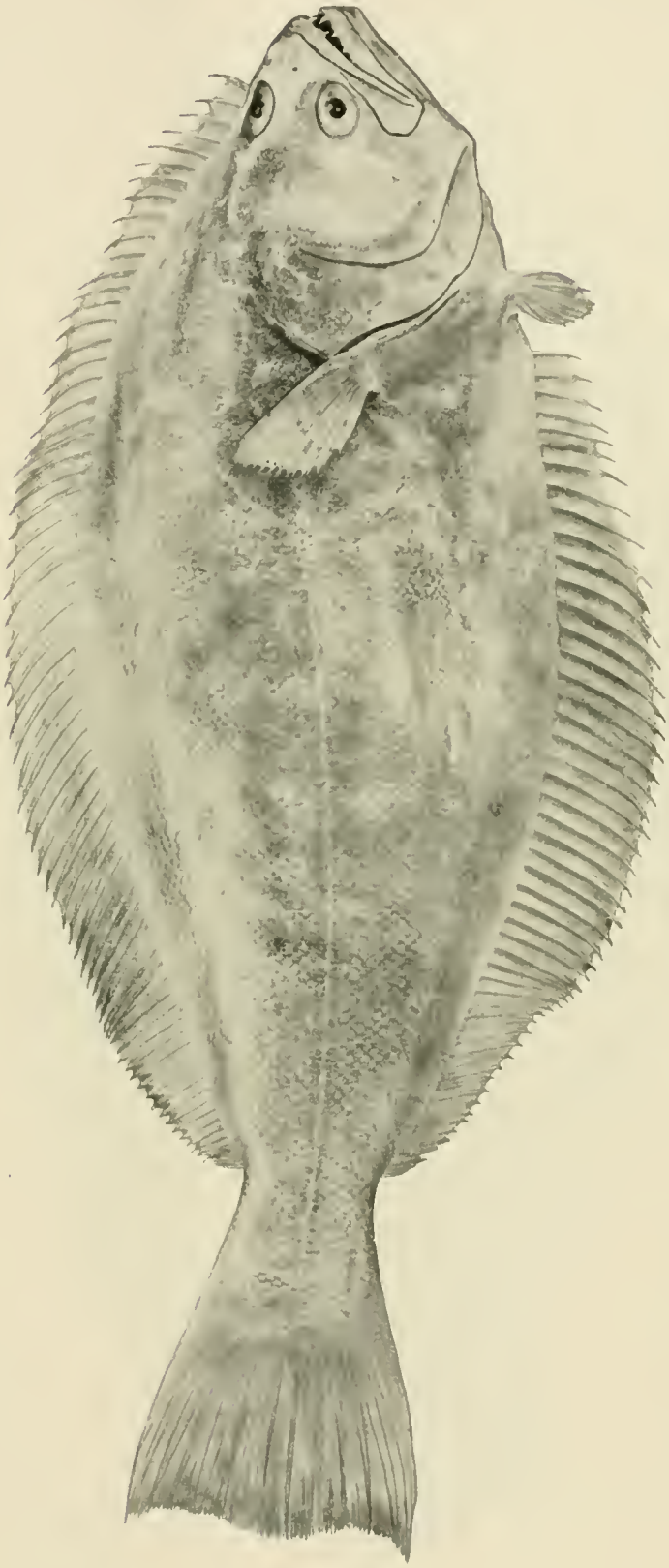

PLATE 9.—*Paralichthys californicus*, from a specimen 300 mm.; U. S. Nat. Mus. 26767; San Diego, Calif.; specimen evidently faded.

PLATE 10.—*Paralichthys aestuarius*, from a specimen 381 mm.; U. S. Nat. Mus. 47280; Gulf of California; specimen probably faded.

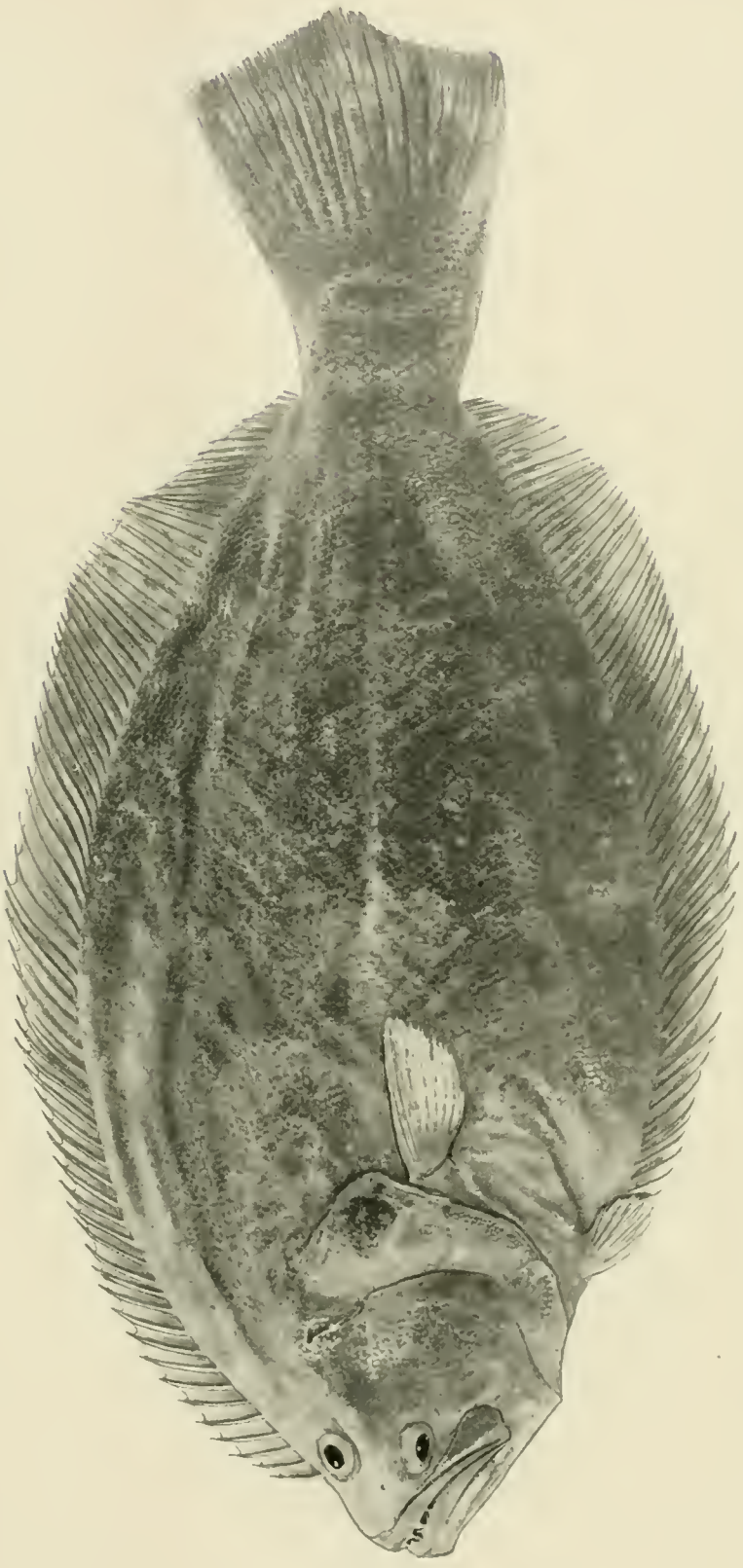

PLATE 11.—*Paralichthys woolmani*, from a specimen 429 mm.; U. S. Nat. Mus. 77705; Paita, Peru; specimen dark, ocellated spots not evident.

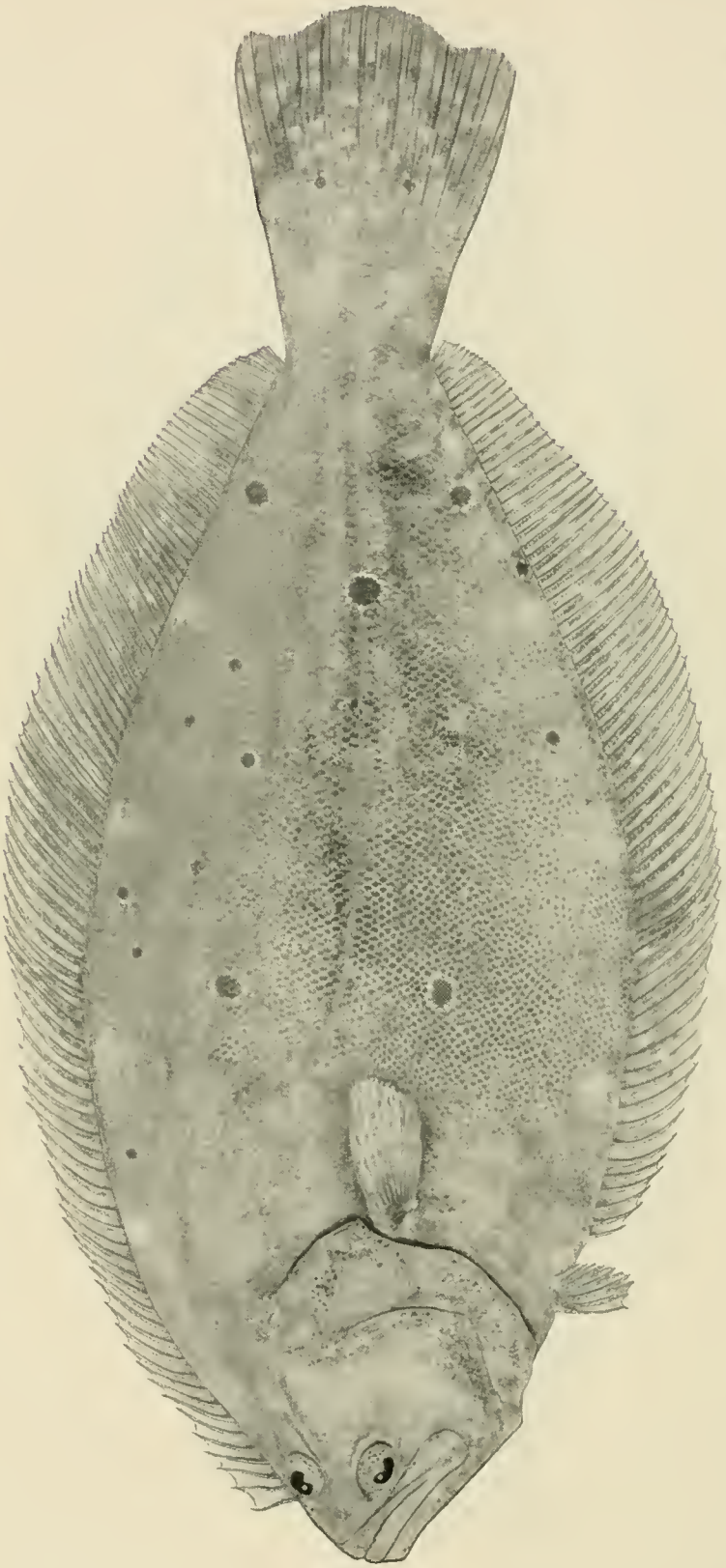

PLATE 12.—*Paralichthys dentatus*, from a specimen 390 mm.; Beaufort, N. C.; ocellated spots in the larger triangle and the others as well, except those in the smaller triangle, somewhat more prominent than usual.

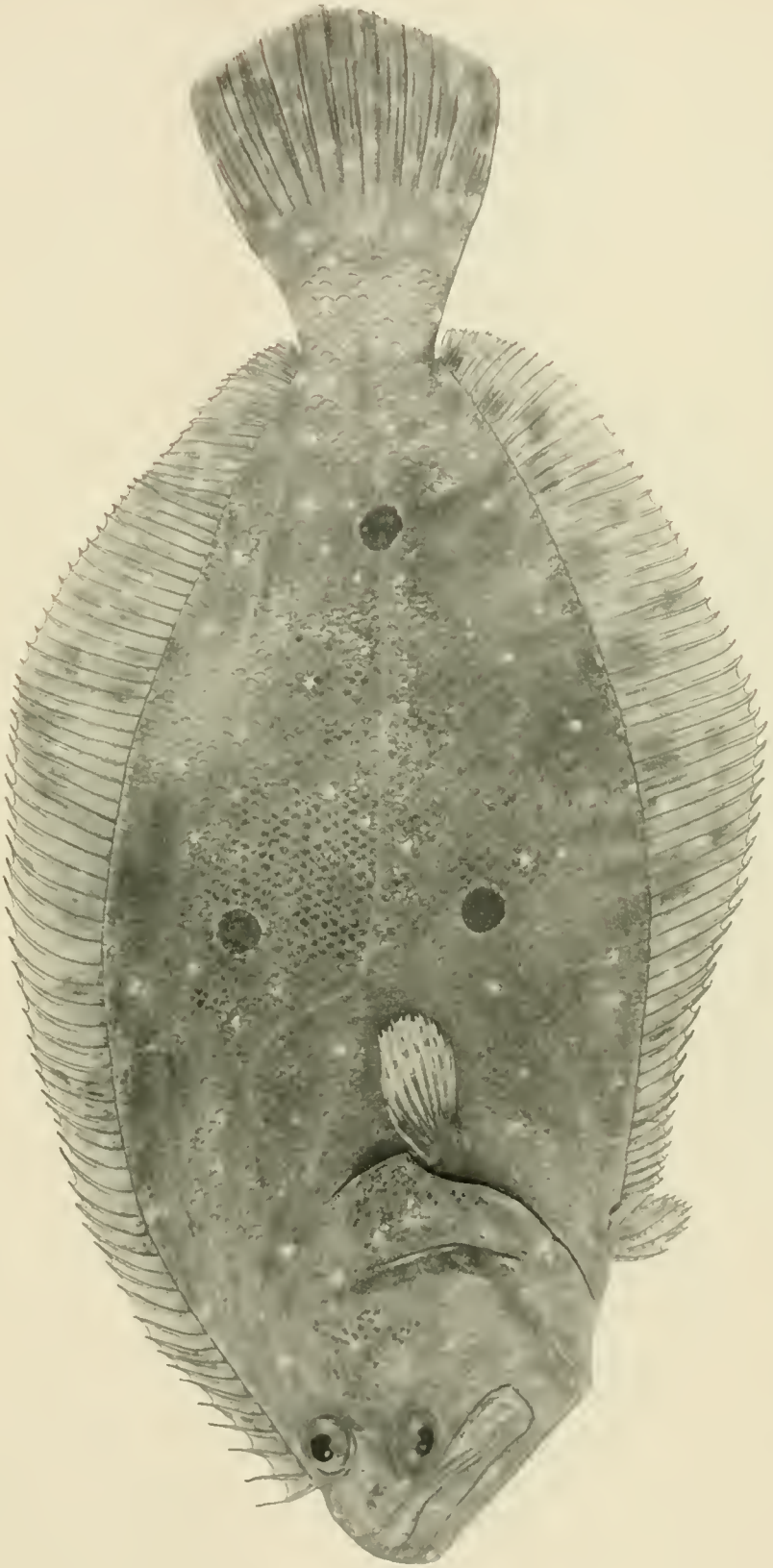

PLATE 13.—*Paralichthys albigutta*, from a specimen 373 mm.; Beaufort, N. C.; spots in large triangle nearly always present and prominent as in figure; spots in small triangle sometimes present, as in *dentatus*, but fainter than in the latter; scattered white spots rather more often present and more prominent in this species, but even in this species absent or obsolescent in most specimens.

PLATE 14.—*Paralichthys tropicus*, from the type, 321 mm.; U. S. Nat. Mus. 34919; off Trinidad, West Indies; specimen evidently faded.

PLATE 15. *Paralichthys lethostigma*, from a specimen 393 mm.; Beaufort, N. C.

UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*
FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

COMPARISON OF YELLOWFIN TUNA OF HAWAIIAN WATERS AND OF THE AMERICAN WEST COAST

By Milner B. Schaefer

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CONTENTS

	Page
Introduction	353
On the selection of regression equations	354
Relative growth of Hawaiian yellowfin tuna	358
Comparison of tuna from Hawaii and from the American west coast	359
Fin lengths	359
Head lengths and distances from snout to fin insertions	362
Other dimensions	371
Counts of gill rakers	371
Discussion	371
Literature cited	373

COMPARISON OF YELLOWFIN TUNA OF HAWAIIAN WATERS AND OF THE AMERICAN WEST COAST

By MILNER B. SCHAEFER, *Fishery Research Biologist*

The yellowfin tuna of the vicinity of the Hawaiian Islands, like the form from the adjacent waters of the American west coast (Schaefer 1948), is here referred to *Neothunnus macropterus* (Temminck and Schlegel) 1842. As has been pointed out previously (Schaefer and Walford 1950), it is possible that the various Pacific forms, the form from the Indian Ocean, and perhaps also those from the Atlantic, should be considered a single species of world-wide distribution. The data presented herein support such a conclusion. This cannot be finally settled until populations from more places have been carefully studied, particularly a series from the Indian Ocean from which was described the specimen of *N. argentivittatus* (Cuvier and Valenciennes) 1831, which should be considered the type of this species.

It is also my opinion that the species now referred to the genera *Thunnus, Neothunnus, Parathunnus,* and *Kishinoella* should all be referred, as has been done by Fraser-Brunner (1950), to a single genus, *Thunnus.* However, since this paper is written to compare the yellowfin tuna from the vicinity of the Hawaiian Islands with the form from the waters adjacent to the American west coast in order to settle the question whether they are racially distinct, questions of taxonomy, synonymy, and nomenclature will be passed over at this time, and for convenience both forms will be referred to the commonly accepted name *N. macropterus.*

The yellowfin tuna is the object of an extensive and intensive fishery along the American west coast from California to the Galapagos Islands. In the Hawaiian Islands there exists a minor fishery that promises to be expanded in the near future to encompass other islands of the mid-Pacific and to increase in intensity in the presently exploited region. Whether the population of the Hawaiian region is part of the same stock of fish as that fished along the American west coast, or is an independent stock, is a question of considerable practical importance: if they are the same stock, the new fisheries would merely add to the strain on the stock already being exploited; if they are independent, there is being tapped an essentially virgin resource.

Schaefer (1948) has published measurement data and counts of denumerable characters on yellowfin tuna from the waters of the Pacific near Costa Rica. Godsil (1948) has published the measurements of a few selected dimensions taken from a very large number of specimens from several sampling localities, extending from the tip of lower California to Panama. Godsil and Byers (1944) have also published gill-raker counts of value to the present study. Those data and those presented herein from the Hawaiian Islands are directly comparable, having been taken in the same manner. Details of measurement methods are given in the papers cited and by Marr and Schaefer (1949). Measurements were made by several field assistants, but all followed identical procedures.

For this study, Hawaiian yellowfin tuna were measured during 1949, between February 21 and September 28. They were selected to give as even a representation as practicable of all sizes of fish available. All specimens were fresh and recently landed from commercial fishing vessels. Most specimens were measured at the Honolulu fresh-fish wholesale auction market, not only a very convenient place to work but almost ideal from a sampling standpoint.

The fish handled there are caught by flag-lines which, by the nature of their operation, sample the fish population very widely. Description of the fishery and the method of handling and marketing the fish will be found in June (1950). Smaller sizes of yellowfin tuna, under about 80 cm. in total length, are seldom taken by the flag-line fishery. These small fish are frequently taken by pole-and-line fishing, in the same manner as on the American west coast,

incidental to fishing for skipjack (*Katsuwonus pelamis*). Specimens of the small sizes were mostly obtained, therefore, from landings at the local tuna cannery, where most of the skipjack catch is landed, particularly during the summer season of good catches. These fish are landed fresh soon after being caught, and are thus comparable to the specimens from the flag-line fishery. The original data on the 203 Hawaiian yellowfin tuna employed in this study are tabulated in table 1. All length measurements are in millimeters, taken as described by Marr and Schaefer (1949). Weights were taken in pounds, because at the auction market the fish were weighed by commercial scales graduated in pounds. Blanks in the table indicate that the measurement or count was not taken on the particular specimen. In addition, a few of the tabulated values were omitted from the analyses, because they were found to deviate more than three standard deviations from the appropriate regression line and seemed probably to be recording errors. These values were as follows:

	Rejected value
1670-mm. specimen, snout to insertion first dorsal	423
1780-mm. specimen, snout to insertion first dorsal	446
1780-mm. specimen, snout to insertion second dorsal	835
1464-mm. specimen, snout to insertion anal	767
1629-mm. specimen, body depth	454
1333-mm. specimen, longest dorsal finlet	34
1259-mm. specimen, length first dorsal spine	97
1397-mm. specimen, length first dorsal spine	129
969-mm. specimen, diameter of iris	26
1605-mm. specimen, diameter of iris	52

Many of the routine computations involved in the analysis of the Hawaiian data, reanalysis of American-west-coast data, and comparison of the two, were performed by Dorothy Dung, whose assistance is gratefully acknowledged.

ON THE SELECTION OF REGRESSION EQUATIONS

It is characteristic of many animals—perhaps of all—that the various parts of the body grow at different rates, so that as the organism increases in size the ratio of one dimension to another changes. For yellowfin tuna this has been demonstrated by Godsil (1948), Schaefer (1948), and Schaefer and Walford (1950). Since this is the case, one cannot use the measurement ratios normally employed in systematic ichthyology for comparing samples of tunas from different places, except in the trivial case where the fish from the two places are of exactly the same size, because differences connected with size could be confused with differences in form of fish of the same size.

In order to avoid this difficulty, the authors of the papers cited above have based their comparisons of samples on the comparison of the regression of one dimension on that of another (usually total length), taken as a measurement of over-all size. This procedure is also employed in the present paper. It may be noted that the efficiency of sampling may be much improved over simple random sampling in such circumstances by selecting the specimens according to total length (the independent variate) to give an even representation of all sizes available so far as is practical; such a sampling scheme was employed in obtaining the data for table 1.

The comparison of body form among fish populations by comparison of regressions would be a simple and straightforward process if the relations between the body dimensions corresponded exactly to the straight lines or simple curves that must be employed in such analyses. Unfortunately, they do not and this may lead to some confusion in the analysis, particularly in situations where one is dealing with small differences and large numbers of specimens. Over restricted ranges of sizes at least, the dimensions of some body parts relative to others seem to be sufficiently well approximated by straight lines (Schaefer 1948, Schaefer and Walford 1950). Large samples of the same size range of the same populations may reveal, however, that regression curves of slight curvilinearity give a better fit to the data, as Godsil (1948) has found for certain dimensions of the American-west-coast yellowfin.

In other cases, such as the fin lengths of yellowfin tuna, the regressions are very strongly curvilinear but may, in some cases at least, be transformed by the allometry equation or other transformation to a linear or nearly linear relation, as has been done in my papers above cited. Whatever the equation employed, however, it is necessary to bear in mind two things. First, the relation employed in the analysis (the mathematical model of the true relation between variables), be it linear or otherwise, is only an approximation to the true relation and as such

does not completely eliminate the effect of size of organism on the character being compared. Second, there sometimes occur rather marked changes in growth rate of one part relative to another at certain sizes, so that a regression which over a considerable range may be represented by a particular equation may not be so represented at all when the range is slightly extended. Indeed, as has been shown by Martin (1949), there seem to be sharp inflection points in the relative-growth curves of several fish species. The avoidance of misleading conclusions demands that these matters be kept in mind in analyses of morphometric data.

TABLE 1.—*Morphometric measurements and counts for Yellowfin tuna* (Neothunnus macropterus) *from the Hawaiian Islands Feb. 21–Sept. 28, 1949*

Total length	Weight	Head length	Snout to insertion first dorsal	Snout to insertion second dorsal	Snout to insertion anal	Snout to insertion ventral	Greatest depth	Taken at dorsal spine No. —	Length pectoral fin	Length first dorsal (first spine)	Length second dorsal	Length anal	Length longest dorsal finlet	Longest dorsal, No. —	Diameter of iris	Length of maxillary	Number of spines first dorsal	Number of dorsal finlets	Number of anal finlets	Number of gill rakers	Sex
	Lb.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		*Mm*	*Mm.*					
451 mm	4.0	128	143	249	272	145	114	7	125	53	50	44	14	5	23	50	14	8+0	8+0	10+20	M
457 mm	4.25	130	148	255	281	146	127	7	134	------	48	38	17	6	25	62	13	8+1	8+0	10+20	F
466 mm	4.5	135	152	263	292	153	125	6	132	54	50	49	15	5	24	55	14	8+2	8+1	10+21	F
466 mm	4.5	137	152	266	294	153	128	7	138	54	54	47	16	6	25	53	14	7+2	7+2	9+20	M
466 mm	5.0	132	153	267	284	148	132	7	130	------	55	49	17	6	25	53	------	8+2	8+2	9+22	M
472 mm	5.0	132	148	265	287	153	130	7	143	56	66	------	16	6	23	55	14	8+2	8+1	9+22	F
476 mm	4.5	136	153	265	295	154	128	6	140	------	53	53	19	6	26	55	13	7+2	7+1	9+20	M
477 mm	4.5	137	156	266	285	153	124	7	135	58	52	52	16	6	25	56	13	7+1	8+0	------	—
477 mm	4.75	138	156	264	290	154	123	7	131	------	55	49	16	5	25	55	------	8+1	8+0	10+20	M(?)
488 mm	5.25	135	168	274	302	157	129	9	149	57	69	54	17	6	24	55	14	8+1	8+0	10+20	M
488 mm	5.5	137	155	269	296	156	132	6	147	------	59	53	16	6	24	54	14	8+0	8+0	10+20	F
493 mm	6.0	142	151	259	302	177	123	8	142	56	56	56	16	5	26	57	13	8+1	8+0	10+21	—
493 mm	5.25	140	154	269	301	157	126	9	146	58	61	60	17	5	26	56	14	8+1	8+1	10+22	M
496 mm	6.0	145	160	274	305	166	133	8	148	57	63	58	16	6	25	57	14	8+1	7+1	10+20	M
497 mm	5.5	138	159	276	303	158	139	7	149	------	58	46	17	5	25	56	13	8+1	8+1	9+22	M
498 mm	5.25	140	161	276	302	161	125	6	151	59	59	52	16	6	26	57	14	8+0	8+1	10+20	F(?)
500 mm	5.0	141	155	274	298	158	125	7	149	56	62	59	18	6	25	57	13	8+1	8+0	9+20	—
501 mm	6.0	142	163	275	307	163	143	6	144	62	52	54	17	6	27	57	12	8+1	8+1	9+20	M
602 mm	5.5	142	163	278	306	158	136	6	152	68	------	51	18	6	25	58	13	8+1	7+2	9+22	M
509 mm	5.0	142	164	277	306	162	132	7	151	59	66	65	19	6	26	58	13	7+2	7+2	9+20	M
509 mm	6.0	146	165	281	309	166	139	10	154	60	66	60	19	5	26	60	13	7+1	7+2	10+21	M(?)
509 mm	6.0	146	165	280	303	159	133	7	145	59	62	62	19	6	27	58	13	8+1	8+0	10+22	M
510 mm	6.0	146	157	283	310	171	128	6	136	62	55	53	20	6	26	60	13	8+1	8+1	------	—
610 mm	6.5	148	168	292	322	170	133	7	154	62	69	65	20	6	27	59	14	7+2	7+1	9+20	M(?)
511 mm	5.5	145	167	282	317	164	135	10	149	58	68	60	17	5	26	58	14	7+2	7+1	9+21	M
525 mm	6.0	145	166	287	311	168	125	8	152	57	------	------	19	5	27	58	14	7+1	7+2	8+21	M
528 mm	6.0	145	168	293	315	168	131	9	145	58	68	65	18	6	25	59	13	8+0	7+1	10+21	—
530 mm	6.0	153	171	294	325	167	133	8	141	60	63	61	18	6	25	58	13	8+0	8+0	9+21	M
530 mm	6.5	154	166	290	310	173	136	9	141	60	68	62	19	6	26	62	14	8+2	8+2	9+20	—
533 mm	6.5	150	166	289	319	171	135	8	156	63	68	61	18	6	26	58	14	8+1	7+1	10+19	M(?)
534 mm	7.6	153	173	302	328	172	144	9	152	------	------	60	18	5	27	60	14	8+1	7+2	8+22	M
625 mm	10	174	189	342	375	196	155	6	191	74	68	72	20	7	30	59	14	8+1	8+1	10+20	F
656 mm	12	180	204	357	393	206	166	8	188	73	83	84	21	6	27	72	13	8+0	8+0	10+20	—
681 mm	------	196	215	377	415	226	172	7	216	84	98	105	------	------	30	81	14	8+1	8+1	------	F
727 mm	16	205	237	396	423	230	184	8	221	78	104	101	28	4	29	78	13	7+1	7+1	10+22	—
755 mm	18.5	207	237	408	452	229	192	8	229	88	113	117	25	6	31	84	13	8+1	8+1	------	—
867 mm	22.0	237	256	456	500	266	205	7	279	101	169	184	28	6	33	92	14	8+1	7+2	9+22	—
882 mm	31.5	228	254	456	500	251	237	9	254	96	149	169	28	6	33	90	14	8+1	8+1	8+21	—
885 mm	31.0	238	272	478	621	271	234	6	258	97	143	142	27	5	33	92	13	7+2	7+2	9+22	—
888 mm	30.0	246	269	475	525	273	232	7	254	107	166	179	34	6	33	98	13	8+1	8+1	9+21	—
912 mm	34	244	275	477	526	274	244	7	265	108	161	171	32	6	34	95	14	8+1	8+1	9+22	—
934 mm	34	260	288	494	551	289	237	7	264	93	139	145	30	5	32	99	14	7+1	7+1	8+21	—
934 mm	35	251	283	497	548	287	241	8	264	102	157	166	29	5	36	101	14	8+1	8+0	8+20	—
940 mm	34.5	247	282	504	550	278	246	7	283	------	160	196	------	------	------	99	14	8+1	8+1	------	—
940 mm	39	259	280	492	559	292	238	------	270	------	157	150	------	------	------	101	------	8+1	8+1	------	—
958 mm	33.5	258	280	497	537	289	231	7	293	113	195	217	38	5	34	101	14	8+1	8+1	10+21	F
969 mm	40.0	255	287	509	557	281	251	7	272	100	143	151	26	6	26	100	13	8+1	8+1	10+21	—
973 mm	39.5	257	291	509	556	289	243	8	278	97	166	184	35	6	34	100	14	8+1	8+1	8+21	—
991 mm	41	260	299	525	575	286	258	8	274	110	156	168	34	6	33	98	14	8+1	7+2	10+20	—
1,004 mm	44	266	302	521	567	279	234	4	303	112	192	201	38	6	35	101	14	8+1	8+1	8+20	M
1,007 mm	46.5	261	289	521	588	298	265	8	285	------	187	217	------	------	------	104	14	8+1	8+1	------	—
1,008 mm	39.5	270	301	523	574	302	240	7	313	110	186	207	36	6	35	105	13	8+1	7+1	10+22	F
1,012 mm	46	272	296	524	597	306	268	7	274	109	190	177	36	6	33	103	13	7+2	7+2	9+20	—
1,016 mm	38	269	278	517	576	304	245	8	258	109	183	192	36	6	33	104	14	8+1	8+1	10+20	—
1,016 mm	43	262	281	530	583	300	258	7	298	117	197	211	36	5	31	104	13	7+2	7+2	9+20	F
1,023 mm	43	262	290	512	592	362	249	9	300	118	190	212	37	7	33	98	14	8+1	7+2	9+22	—
1,043 mm	49	268	309	538	593	305	257	7	315	111	202	209	38	6	33	102	13	8+1	8+1	9+21	—
1,045 mm	46	268	307	545	593	303	269	7	322	112	199	215	39	5	32	105	14	8+1	7+2	10+21	M
1,064 mm	52	277	307	546	605	315	271	9	306	107	205	218	37	6	32	105	14	7+2	8+1	8+22	—
1,077 mm	49	282	314	570	622	322	267	7	309	127	229	232	40	7	35	108	13	8+1	8+1	10+20	—
1,081 mm	48	290	320	556	626	323	263	7	283	119	183	185	39	6	36	109	14	8+1	8+0	10+21	—
1,086 mm	53	285	314	561	617	321	273	8	294	124	196	198	36	6	34	108	13	8+0	8+1	8+22	—
1,090 mm	50	293	329	566	621	333	269	5	286	115	170	180	37	6	35	109	13	8+1	8+1	9+22	—
1,090 mm	51	286	316	557	606	325	269	8	319	126	205	246	39	6	36	111	13	8+1	8+1	9+21	—
1,132 mm	58	288	322	580	636	319	293	7	323	------	210	236	43	6	36	110	14	8+1	8+1	9+21	—
1,134 mm	60	285	330	591	639	315	295	8	311	114	206	240	34	6	35	110	14	8+1	8+1	9+20	—
1,142 mm	63	304	342	596	651	340	289	9	310	121	231	248	41	6	35	115	14	8+1	8+1	8+20	—
1,170 mm	66	311	336	596	677	349	292	9	305	119	204	210	40	7	34	117	14	8+1	8+0	9+21	—
1,172 mm	66	292	330	591	661	325	291	9	332	128	322	336	44	6	37	111	14	8+1	8+1	9+21	—
1,179 mm	70	301	323	593	657	340	295	9	350	118	249	262	40	5	34	117	14	8+2	8+1	9+21	—

TABLE 1.—*Morphometric measurements and counts for Yellowfin tuna* (Neothunnus macropterus) *from the Hawaiian Islands Feb. 21–Sept. 28, 1949*—Continued

Total length	Weight	Head length	Snout to insertion first dorsal	Snout to insertion second dorsal	Snout to insertion anal	Snout to insertion ventral	Greatest depth	Taken at dorsal spine No. —	Length pectoral fin	Length first dorsal (first spine)	Length second dorsal	Length anal	Length longest dorsal finlet	Longest dorsal, No. —	Diameter of iris	Length of maxillary	Number of spines first dorsal	Number of dorsal finlets	Number of anal finlets	Number of gill rakers	Sex
	Lb.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		*Mm.*	*Mm.*					
1,206 mm	75	309	342	605	685	346	299	9	336	133	278	315	43	6	38	122	13	8+1	8+1	7+19	—
1,217 mm	76	313	346	621	693	358	305	7	370	146	305	327	45	5	37	117	14	8+1	8+1	9+20	—
1,238 mm	75	310	348	621	694	351	300	9	342	136	359	267	43	6	37	120	14	8+1	8+1	8+20	—
1,238 mm	80	311	342	624	703	352	303	10	341	134	280	303	44	6	37	118	13	8+1	8+1	9+21	—
1,239 mm	84	307	343	615	681	339	316	9	344	131	274	294	44	7	37	118	14	8+1	8+1	8+21	—
1,240 mm	78	317	351	629	702	355	297	7	341	131	276	293	45	6	33	121	13	8+1	8+1	8+19	—
1,255 mm	86	314	357	645	700	357	319	9	336	142	276	310	42	6	38	124	13	8+1	8+1	9+20	—
1,256 mm	86	324	356	650	720	370	320	8	375	136	278	306	42	5	37	129	14	8+1	8+1	9+21	M
1,258 mm	88	314	356	629	689	351	310	7	343	149	284	355	45	5	39	126	13	8+1	8+1	9+20	—
1,259 mm	82	317	358	632	702	358	303	9	349	97	348	363	51	7	38	124	13	8+2	8+1	10+22	—
1,278 mm	85	311	343	629	702	346	313	10	349	143	298	311	46	5	39	115	13	8+1	8+1	9+20	—
1,287 mm	86	313	353	648	720	357	309	7	348	141	331	377	45	5	40	124	14	8+1	8+1	9+22	F
1,288 mm	88	318	359	645	716	365	309	10	359	142	351	398	46	6	38	121	14	8+1	8+1	9+21	—
1,289 mm	88	328	376	645	729	365	325	10	337	134	320	332	49	5	38	129	14	8+1	8+1	9+21	—
1,297 mm	85	330	363	659	723	372	325	7	354	145	270	337	45	6	37	131	14	8+1	8+1	9+21	F
1,297 mm	90	324	358	643	706	366	313	9	353	141	337	387	50	5	38	125	13	8+1	8+1	9+21	—
1,299 mm	85	323	353	648	716	363	304	9	365	132	358	382	44	6	39	125	14	7+2	8+1	10+21	—
1,313 mm	98	330	361	657	741	366	318	8	369	149	367	370	47	4	39	129	13	8+1	7+1	9+21	—
1,323 mm	96	329	369	668	752	377	321	8	340	139	354	387	46	6	37	127	13	8+2	7+2	9+20	F
1,323 mm	97	329	357	655	730	371	327	6	367	148	397	458	53	5	40	127	13	7+2	7+2	9+21	—
1,323 mm	101	340	360	662	746	396	335	11	336	151	359	372	44	5	38	128	14	8+1	8+1	9+22	—
1,325 mm	99	333	364	676	740	374	325	7	338	137	307	335	50	6	37	131	13	8+1	8+1	------	------
1,327 mm	104	342	377	679	737	381	337	7	367	162	306	323	46	6	38	135	13	8+2	8+1	------	------
1,330 mm	100	335	363	670	757	381	330	8	354	162	385	437	51	6	40	126	14	7+2	7+1	9+20	------
1,331 mm	99	331	372	668	732	373	342	9	378	152	305	342	47	6	38	128	14	8+1	8+1	9+21	------
1,332 mm	93	327	362	661	733	365	306	9	366	146	318	385	47	5	40	128	13	8+2	8+1	10+21	------
1,333 mm	98	336	369	665	746	376	316	6	345	135	275	289	34	5	35	126	14	7+2	7+2	------	------
1,337 mm	95	338	379	670	734	375	326	9	349	148	344	365	46	6	39	131	14	8+2	8+1	8+21	------
1,339 mm	92	324	366	669	741	364	307	7	355	142	317	354	40	6	36	128	13	8+1	8+0	9+20	F
1,339 mm	100	330	367	652	742	366	312	11	355	153	386	388	54	7	40	131	13	8+2	8+1	8+21	M
1,344 mm	99	334	367	667	752	375	312	9	367	131	327	342	49	4	38	130	14	8+1	7+2	8+21	------
1,352 mm	112	333	368	668	751	372	348	10	363	145	406	425	54	5	39	132	13	7+2	7+2	9+21	------
1,353 mm	93	337	375	671	752	378	329	9	335	146	349	450	46	5	40	127	13	7+2	7+2	9+20	------
1,358 mm	108	333	381	689	775	384	350	7	368	157	363	364	45	5	40	132	14	8+0	8+1	9+20	------
1,359 mm	120	335	367	673	747	378	361	7	372	145	350	374	53	6	40	135	14	8+1	8+1	9+21	M
1,371 mm	99	337	376	692	762	380	319	9	353	------	337	348	42	5	38	129	13	8+2	8+1	------	F
1,371 mm	114	344	378	695	779	405	353	10	356	164	244	334	49	5	37	133	13	8+1	8+1	9+21	F
1,378 mm	110	345	387	694	759	379	347	9	361	155	323	351	52	5	39	134	13	8+1	8+1	9+19	M
1,380 mm	107	342	382	686	755	392	337	6	341	147	377	409	50	6	39	129	13	8+2	8+1	9+21	F
1,385 mm	121	348	377	711	792	393	354	8	370	175	336	401	50	6	41	136	14	8+1	8+0	10+21	------
1,391 mm	110	346	389	698	772	396	346	7	380	139	371	395	50	4	38	134	13	8+1	8+1	10+21	F
1,391 mm	112	346	403	706	781	396	339	8	342	147	304	319	51	6	38	132	13	7+2	8+1	10+21	------
1,396 mm	113	336	372	685	776	379	345	10	360	138	404	447	56	7	39	127	14	8+1	8+1	9+20	F
1,397 mm	123	349	401	706	792	400	365	9	361	129	345	352	48	6	37	134	13	8+2	8+1	9+22	M
1,397 mm	124	354	391	707	777	395	364	8	350	167	308	367	57	6	41	139	13	8+1	8+1	9+20	M
1,399 mm	116	340	371	700	780	382	341	8	341	151	383	420	54	5	39	132	14	8+1	8+1	9+21	F
1,405 mm	116	346	394	709	783	397	344	8	350	156	406	459	51	6	39	137	14	8+1	7+1	8+21	------
1,409 mm	136	346	397	713	788	391	371	10	362	157	470	495	54	6	41	135	13	8+2	8+1	9+20	M
1,413 mm	116	346	396	712	786	394	346	9	368	158	428	505	50	5	40	136	13	8+2	8+1	9+20	F
1,423 mm	128	356	405	715	798	401	357	8	358	161	467	532	51	6	40	142	13	8+2	8+1	8+19	—
1,429 mm	128	352	396	719	785	394	353	11	359	155	309	363	44	5	39	135	13	8+1	8+1	10+20	F
1,429 mm	133	355	388	705	796	401	363	9	355	162	417	500	45	5	41	141	------	7+2	8+1	8+21	—
1,431 mm	122	362	403	724	799	414	362	7	367	151	341	360	50	5	38	131	14	8+2	8+1	10+21	M
1,435 mm	133	360	403	720	816	407	371	7	391	173	466	487	52	6	41	145	13	9+1	8+1	------	------
1,437 mm	122	351	389	703	794	393	346	9	377	168	462	505	54	5	42	131	13	8+1	8+1	10+21	------
1,438 mm	117	362	397	732	804	412	338	11	381	174	418	427	49	6	39	138	14	8+2	7+1	------	------
1,441 mm	123	355	399	726	811	404	350	10	350	155	380	490	51	4	39	143	13	7+2	8+1	11+21	F
1,441 mm	131	352	392	702	776	392	369	8	382	157	512	541	58	6	41	137	13	8+1	8+1	10+20	------
1,444 mm	126	351	402	729	794	391	350	6	368	171	406	460	44	6	40	136	13	8+2	8+1	9+22	------
1,455 mm	131	359	407	741	805	409	358	------	376	169	405	443	51	6	38	141	------	8+2	8+2	9+20	------
1,457 mm	133	363	394	750	807	398	367	6	351	148	303	363	58	6	39	137	14	8+1	8+1	9+21	------
1,464 mm	123	347	385	696	767	400	371	9	376	145	465	561	50	6	41	139	14	9+1	9+1	------	M
1,465 mm	125	374	402	726	822	423	350	7	368	173	335	365	51	6	43	141	13	8+1	8+1	9+20	F
1,466 mm	136	361	403	750	816	408	369	7	342	183	432	521	51	6	40	140	14	8+2	8+1	9+21	M
1,474 mm	135	366	404	733	799	408	379	8	362	167	372	512	59	6	42	142	13	8+2	8+1	9+22	M
1,480 mm	148	376	412	750	837	421	388	9	386	177	452	503	55	6	42	149	13	7+1	8+1	9+20	M
1,486 mm	134	364	409	739	835	413	365	7	377	169	442	520	52	5	40	149	14	8+2	8+2	10+22	F
1,488 mm	143	367	395	726	825	428	375	8	372	165	569	645	65	7	43	143	14	8+2	8+1	8+20	F
1,506 mm	135	368	422	760	851	413	383	10	389	175	430	466	49	4	40	147	13	8+1	8+1	8+22	F
1,514 mm	163	369	423	764	826	415	412	8	394	158	466	493	63	5	41	144	13	8+2	8+1	9+20	------
1,517 mm	139	386	416	748	836	437	373	6	375	176	587	687	56	5	44	144	14	8+1	7+2	9+20	M
1,518 mm	165	372	404	742	859	417	386	10	370	169	417	464	55	5	39	145	13	8+1	8+1	8+21	M
1,520 mm	158	366	414	766	830	412	386	10	390	169	521	557	57	6	42	144	13	8+1	8+1	10+20	------
1,521 mm	146	372	400	742	832	421	377	9	377	178	517	580	64	5	42	143	14	8+1	8+1	9+21	------
1,534 mm	162	378	421	761	833	422	403	11	396	------	605	665	60	4	45	144	13	8+2	8+1	9+20	------
1,548 mm	157	397	432	777	858	441	409	7	380	177	465	465	53	5	43	152	14	8+2	8+1	9+23	M
1,550 mm	177	383	420	769	852	430	416	9	379	188	540	527	57	6	44	148	13	8+2	8+1	8+19	M
1,556 mm	180	385	428	804	879	440	412	9	392	175	566	617	58	4	45	152	13	8+2	8+1	8+19	—
1,564 mm	153	404	439	798	885	452	388	8	376	193	548	650	58	7	44	157	13	8+2	8+2	9+20	M
1,579 mm	169	398	435	779	880	459	399	8	368	164	382	424	53	6	44	149	13	8+1	8+1	11+21	M
1,581 mm	179	387	434	783	888	441	400	8	381	162	437	481	56	5	40	148	13	8+2	8+2	9+20	M
1,582 mm	166	389	443	789	881	437	392	6	397	187	647	803	61	6	45	156	13	7+1	7+2	------	—
1,584 mm	182	392	430	789	864	440	421	7	382	169	502	570	55	7	42	150	14	8+2	8+1	10+21	M
1,604 mm	201	394	431	806	884	447	430	11	394	190	560	668	63	6	43	152	13	8+2	8+1	9+21	------
1,605 mm	202	396	446	782	892	444	425	10	387	152	372	556	60	6	52	151	13	8+2	8+1	10+20	M

TABLE 1.—*Morphometric measurements and counts for Yellowfin tuna* (Neothunnus macropterus) *from the Hawaiian Islands Feb. 21–Sept. 28, 1949*—Continued

Total length	Weight	Head length	Snout to insertion first dorsal	Snout to insertion second dorsal	Snout to insertion anal	Snout to insertion ventral	Greatest depth	Taken at dorsal spine No. —	Length pectoral fin	Length first dorsal (first spine)	Length second dorsal	Length anal	Length longest dorsal finlet	Longest dorsal, No. —	Diameter of iris	Length of maxillary	Number of spines first dorsal	Number of dorsal finlets	Number of anal finlets	Number of gill rakers	Sex
	Lb.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		*Mm.*	*Mm.*					
1,611 mm	163	393	432	796	883	445	393	7	368	184	390	664	62	6	45	156	14	8+1	8+1	9+21	
1,614 mm	201	399	445	811	877	440	440	8	400	184	567	627	65	5	44	153	14	8+1	8+1	9+21	M
1,621 mm	176	405	430	785	902	452	408	9	380	192	438	495	63	6	44	157	14	8+2	8+1	9+21	M
1,629 mm	212	415	447	822	907	457	427	10	400	185	453	700	63	5	45	158	13	8+1	8+1	9+18	M
1,629 mm	220	411	455	829	905	457	454	7	422	165	614	672	62	5	42	151	13	8+2	8+1	9+20	M
1,631 mm	201	412	459	810	901	468	437	10	396	203	554	592	70	5	45	156	13	8+1	8+1	8+21	M
1,635 mm	211	403	470	811	895	457	452	9	390	195	651	745	63	7	45	154	13	8+1	8+1	10+20	M
1,636 mm	209	399	447	813	890	442	443	7	401	195	603	682	64	6	43	153	13	8+1	8+1	9+19	M
1,638 mm	172	401	442	810	901	451	389	11	417	194	586	702	60	5	45	152	14	7+2	7+2	10+21	
1,639 mm	200	404	454	812	889	448	432	8	440	179	540	603	66	6	45	150	13	8+2	8+1	8+20	M
1,640 mm	192	403	444	813	890	442	427	9	370	206	760	850	67	6	48	153	14	8+1	8+1	8+20	M
1,641 mm	206	402	442	809	896	450	438	10	408	189	564	644	61	4	44	157	14	7+2	7+2	9+17	M
1,642 mm	195	403	445	797	910	451	426	10	406	192	604	615	62	6	44	154	13	8+1	8+1	9+20	
1,643 mm	200	404	442	822	915	453	432	11	390	184	490	510	63	7	42	156	14	8+2	8+0	8+21	
1,648 mm	209	408	448	808	919	449	445	8	440	180	624	720	69	6	44	161	13	8+2	8+1	8+21	M
1,654 mm	201	408	458	820	913	454	427	9	394	196	703	725	64	5	45	153	13	8+1	8+1	9+21	M
1,659 mm	201	401	444	818	903	449	428	8	383	181	639	716	63	6	46		13	8+2	8+1	8+21	M
1,660 mm	204	404	447	827	907	453	429	7	415	200	654	620	63	6	45	159	13	8+2	8+1	9+19	M
1,662 mm	208	409	446	814	916	460	435	8	406	187	555	579	68	6	45	163	13	8+2	8+1	9+20	M
1,665 mm	203	399	456	825	910	453	437	8	395	196	602	685	65	6	46	158	13	8+1	8+1	9+20	
1,665 mm	205	400	451	835	923	443	428	10	430	200	527	688	64	5	45	150	13	8+2	8+1	9+21	M
1,670 mm	200	414	464	822	924	464	417	10	399	190	644	790	66	5	47	158	13	8+2	8+1	9+21	—
1,670 mm	205	414	423	803	902	483	422	6	407	200	668	759	65	6	47	158	13	8+2	8+1	10+21	—
1,673 mm	201	408	457	829	914	456	419	9	377	185	592	676	64	6	45	158	13	8+1	8+1	8+20	
1,674 mm	193	412	461	850	917	464	420	8	402	199	683	715	64	6	45	161	13	8+2	8+1	9+20	
1,674 mm	209	410	450	827	908	459	450	7	414	185	560	607	62	6	44	154	13	9+1	8+1	9+20	M
1,676 mm	196	411	449	817	919	462	423	11	412	207	661	732	60	5	46	157	13	7+2	8+1	9+21	
1,677 mm	192	419	447	829	923	469	438	7	382	186	634	753	62	6	47	167	14	8+1	8+0	9+20	M
1,682 mm	209	421	455	845	907	475	408	6	380	196	590	684	65	5	45	169	13	8+2	8+1	9+19	
1,696 mm	215	411	462	844	920	462	427	7	394	170	604	596	68	5	42	160	13	7+2	8+1	9+21	M
1,700 mm	214	410	461	841	918	452	443	7	389	188	615	657	68	5	46	162	13	8+1	8+1	9+20	M
1,700 mm	215	410	453	839	927	455	435	6	398	186	594	714	62	6	45	160	13	8+2	8+1	10+21	M
1,700 mm	216	430	483	849	927	486	440	8	431	204	670	722	65	5	46	174	13	8+1	8+1	9+20	M
1,703 mm	205	411	460	847	923	462	429	10	442	203	607	536	71	6	46	160	13	8+1	8+2	9+21	
1,703 mm	225	419	463	848	941	474	451	11	432	196	553	584	69	7	43	160	13	8+1	8+1	9+21	M
1,705 mm	222	414	459	835	919	464	430	10	392	186	567	565	67	6	43	156	14	8+1	8+1	9+20	
1,714 mm	227	420	460	838	930	463	462	9	420	191	598	648	69	6	45	158	13	8+2	8+1	9+21	M
1,716 mm	219	417	458	845	930	472	451	8	398	185	668	733	69	6	46	163	13	8+1	8+1	8+20	M
1,717 mm	229	415	471	846	938	473	445	8	402	197	634	742	64	5	45	156	13	8+2	8+1	10+20	M
1,718 mm	227	408	450	830	935	460	438	11	414	175	614	651	65	6	43	154	14	8+1	8+1	10+21	M
1,721 mm	221	439	476	861	953	480	425	10	422	184	444	522	62	5	46	171	13	7+2	7+1	9+20	
1,723 mm	223	411	468	832	923	466	452	9	431	190	601	565	60	5	44	158	13	8+1	8+1	7+18	
1,724 mm	224	419	469	850	939	476	447	10	401	196	583	611	67	6	42	162	13	8+2	8+2	9+21	M
1,734 mm	212	416	449	847	935	463	432	9	420	174	712	742	70	5	45	157	13	8+1	8+1	8+21	M
1,748 mm	238	419	451	847	955	470	447	10	402	187	630	693	61	6	46	159	14	8+2	8+1	9+21	
1,778 mm	236	423	466	866	953	491	456	8	417	208	647	634	72	6	45	166	13	8+2	8+1	9+21	M
1,780 mm	230	418	446	835	948	470	452	10	398	192	688	781	72	5	52	165	13	8+1	8+2	10+20	M
1,785 mm	230	430	487	889	960	485	455	10	416	211	777	836	72	5	48	168	14	8+1	8+1	9+19	M

Godsil (1948), whose work will be discussed subsequently, has found that a curvilinear equation fits the regressions on body length of the distances from the tip of the snout to various fin insertions and head length rather better than a linear one. He also discovered that when he fitted regression equations of the selected type to each of several samples from the same region, and also fitted an equation of this same type to the pooled data of all such samples, the individual regressions differed from the regression for the pooled data to a greater extent than might be expected from purely random variation. This he attributed to a lack of "biological homogeneity" (which he contrasts to "statistical homogeneity") within the stock of fish sampled, arising from incomplete mixing of fish from different spawning grounds. This may indeed be true. A rather simpler explanation is that the small differences he found between regressions among the samples from the same region are due to rather great differences in size composition of the several samples and the necessarily approximate nature of the regression equations employed. Whatever the cause, it is necessary to recognize that such differences can and do arise and to take suitable account of them where required, both in the sampling and in the subsequent analysis. By drawing samples widely from many different schools within the region to be studied, one minimizes for purpose of comparison the effects, if any, of lack of "biological homogeneity" by including in the variance of the sample any differences between subdivisions of the population with different genetic histories. By comparing only samples of

the same size range from different regions, one will tend to reduce the apparent difference due to the failure of the regression equation employed to completely correct for differences in size composition of the samples.

There is probably no purely routine method of analysis which may be safely employed in comparing body dimensions of tunas from different regions. The selection of regression equations, and the application of other statistical techniques, should be undertaken with proper consideration of the particular data at hand, the hypotheses regarding it that are to be tested, and the precision required in each particular case.

RELATIVE GROWTH OF HAWAIIAN YELLOWFIN TUNA

Schaefer (1948) and Schaefer and Walford (1950) fitted linear regression lines to head length and distances from tip of snout to insertions of the first dorsal, second dorsal, anal, and ventral fins plotted against total length for yellowfin tuna from the west coast of Central America and from the Atlantic coast of Africa. Godsil (1948) found more extensive data on the same dimensions of yellowfin from the American west coast to be better fitted by a regression line of slight curvilinearity. To the Hawaiian data have been fitted linear regressions, the constants for which are given in table 2, as well as curvilinear regressions of the type selected by Godsil. Equations for the latter and corresponding standard errors of estimate (s) about them are as follows:

Head length	$y=69.54+0.20805x-15419/x$	$s=6.02$
Snout to insertion first dorsal	$y=80.34+0.22868x-16997/x$	$s=7.77$
Snout to insertion second dorsal	$y=17.28+0.48226x+11445/x$	$s=10.94$
Snout to insertion ventral	$y=78.87+0.23340x-16778/x$	$s=7.96$
Snout to insertion anal	$y=109.92+0.49037x-25129/x$	$s=9.32$

Over the range of sizes in our sample, the curvilinear regressions result in slightly smaller variances about them than the linear regressions; but, as may be seen from the above equations or from the graphs in the next section (figs. 6–10), the differences between these curves and straight lines are slight. Indeed, for snout to second dorsal insertion the slight curvature of the regression is opposite in direction to those fitting the data of other dimensions and to that of Godsil for his American-west-coast fish (fig. 8). Furthermore, the difference between the linear and curvilinear regressions for this dimension is, for the Hawaiian data, such as might arise by chance alone in between 1 in 20 and 1 in 100 cases.

The relations between body depth and total length, diameter of iris and head length, and length of maxillary and head length seem to be well described by linear regressions over the entire size range. The statistics of these regressions are tabulated in table 2.

In each of these cases where linear regressions fit the data, the y intercept of the regression line differs significantly from zero. Furthermore, except for depth of body on total length and length of maxillary on head length, the difference is sufficiently great that the expression as ratios of the relation between variables would result in a considerable error from this source. This

TABLE 2.—*Statistics of linear regressions of measurements of Hawaiian* N. macropterus

All logarithms are to base 10.
N=number in sample.
$\bar{x}$, $\bar{y}$=means of x and y.
Sx^2, Sy^2, Sxy are sums of squares and products of deviations from the means $\bar{x}$, $\bar{y}$.
$b=\frac{Sxy}{Sx^2}$=regression coefficient of y on x.
$s^2=\frac{Sy^2-b^2Sx^2}{N-2}$=estimate of variance about regression line.

Independent variable x	Dependent variable y	N	$\bar{x}$	$\bar{y}$	Sx^2	Sy^2	Sxy	b	s
Total length	Head length	203	1247	314	32,985,274	1,688,363	7,443,781	0.22567	6.51
Do	Snout to insertion first dorsal	201	1242	348	32,516,976	2,016,613	8,071,090	.24821	8.17
Do	Snout to insertion second dorsal	202	1244	628	32,699,372	7,221,223	15,340,597	.46914	11.03
Do	Snout to insertion ventral	203	1247	354	32,985,274	2,118,502	8,331,748	.25259	8.34
Do	Snout to insertion anal	202	1246	697	32,937,786	8,906,792	17,108,301	.51941	10.14
Do	Greatest body depth	202	1245	316	32,838,336	2,162,089	8,363,540	.25469	12.64
Head length	Diameter of iris	198	315	37.6	1,667,677	9,005	119,469	.07164	1.51
Do	Length of maxillary	203	314	121.8	1,688,191	244,663	640,453	.37937	2.90
Log total length	Length pectoral	203	3.06448	324	6.52772	1,617,580	3211.2003	491.93	13.73
Do	Log length second dorsal [1]	172	3.13093	2.55442	1.54087	8.11623	3.41003	2.21305	.0579
Do	Log length anal [1]	172	3.13093	2.59682	1.54087	8.66325	3.52758	2.28934	.0588
Do	Log length first dorsal spine	188	3.07798	2.12768	5.42218	5.30176	5.30154	.97775	.02530
Do	Log length longest dorsal finlet	198	3.06657	1.62583	6.44930	7.67031	6.94360	1.07664	.03146
Do	Weight in pounds	202	3.06566	1.82955	6.47257	58.24926	19.39100	2.99587	.02793

[1] Only specimens 600 mm. and over in total length.

result is similar to that obtained from Central American and African yellowfin tuna (Schaefer 1948, Schaefer and Walford 1950) and illustrates again the generalization that, owing to differential growth rates, comparison of dimensions expressed as ratios is invalid for yellowfin tuna.

Also similar to previous Central American and African results, is the finding that the growth of the pectoral fin of Hawaiian yellowfin tuna is such that over the entire range of sizes available in our sample, the relation between length of fin and total length is well described by the equation

$$y=491.9 \log x-1184,$$

a linear regression giving a good fit to the length of fin plotted against logarithm of total length. The regression statistics are given in table 2.

For Central American and African fish, the lengths of second dorsal and anal fins plotted against total length were found to be fitted by an equation of the type $y=ax^b$, so that a linear regression was obtained by plotting logarithms of fin length against logarithms of total length. The sizes of fish involved were from about 50 cm. to 160 cm. in total length for the fish from both regions. For Hawaiian yellowfin tuna, a linear relation between logarithm of fin length and logarithm of fish length provides a fairly good fit over the range of sizes 60 cm. to 178 cm., but when smaller sizes are included, the regression is obviously curvilinear (fig. 2 and 3). Linear-regression equations were fitted, for comparative purposes, only to the data for fish 60 cm. and over in total length, the results being tabulated in table 2. To provide a reasonable fit to the data for all sizes, however, the second-degree polynomials illustrated in the figures were fitted, the equations being, for logarithms of length of second dorsal (y_1) on logarithm of total length (x_1),

$$y_1=7.64965-5.59555x_1+1.26613x_1^2 \qquad s=.05238$$

and for logarithm of length of anal (y_1) on logarithm of total length (x_1)

$$y_1=4.79192-3.82511x_1+0.99707x_1^2 \qquad s=.03607$$

It is obvious that the relative rates of growth of the second dorsal and the anal fins accelerate very rapidly with increase in size of fish, the large fish having, relatively, enormously longer fins.

The equation $y=ax^b$ was found to provide a good fit to our Hawaiian data over the entire range of sizes for length of longest dorsal spine (the first spine in each specimen) and length of longest dorsal finlet relative to total length, the logarithms of the dimensions plotted against logarithm of total length being well fitted by linear regressions, the constants for which are given in table 2. In previous studies of Costa Rican and African fish, linear regressions were found adequate for these relations over the size range 50 cm. to 160 cm., and for only that range of sizes it would be difficult to perceive that the allometry equation provides a better fit to the Hawaiian data. The availability of a longer range of sizes from Hawaiian waters made it possible to observe the slightly curvilinear nature of the relation. How little it differs from a straight line may be seen from the closeness to unity of the values of b tabulated in table 2 for these regressions.

The weight of Hawaiian yellowfin varies almost exactly as the cube of the length, the relation between length in millimeters (x) and weight in pounds (y) being expressed by the equation

$$\log y=2.996x-7.35477$$

COMPARISON OF TUNA FROM HAWAII AND FROM THE AMERICAN WEST COAST

Fin lengths

The most outstanding differences revealed by this study between yellowfin tuna from Hawaii and those from waters off Costa Rica are the relative lengths of the pectoral, second dorsal, and anal fins. There seem also to be small but dependable differences in length of longest dorsal spine and length of longest dorsal finlet.

Figure 1 illustrates the relation between length of pectoral fin and total length for Hawaiian and Costa Rican fish. The points plotted in this figure, and in the other figures in this paper, do not represent individual fish but are the mean values of the two variables for each 10-cm. size category. This method of plotting recommends itself because the data for individual fish are too numerous to be clearly depicted. It has also the advantage of making possible a visual comparison of mean values of the dimension under consideration for fish of each single 10-cm. size category from the two populations. The inherent disadvantage is, of course, that each point does not represent the same number of fish, so that their positions are of varying degrees of reliability. The regression

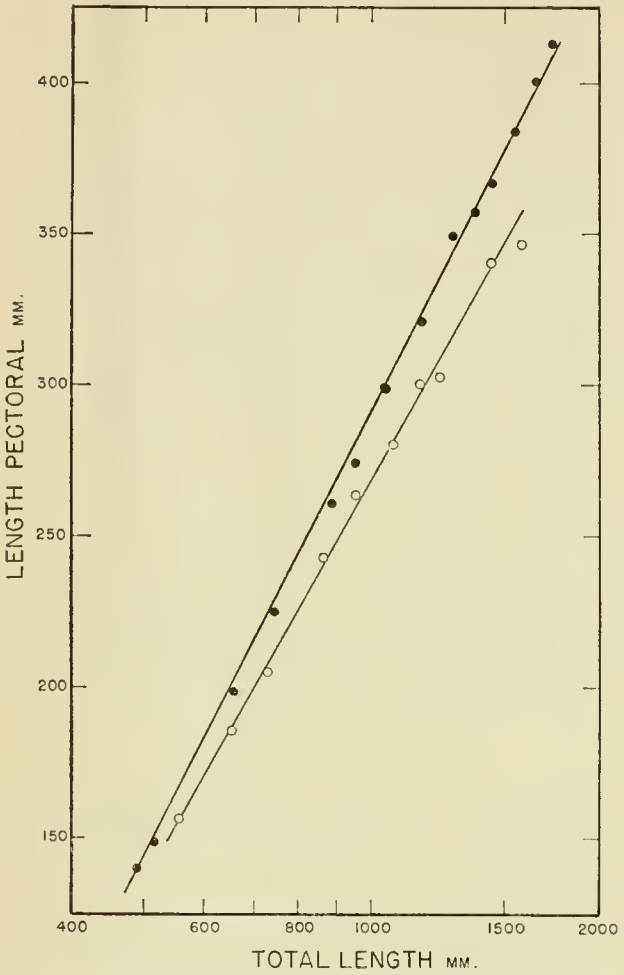

FIGURE 1.—Relations between length of pectoral fin and total length. Open circles and fine line represent Costa Rican data. Solid circles and heavy line represent Hawaiian data.

lines depicted in the figures were in every case fitted to the original data and not to the class means.

As may be seen from figure 1, the pectoral fins of Hawaiian yellowfin tuna, over the size range considered, are on the average longer than those of Costa Rican fish, and the difference increases as the size of fish increases. No elaborate statistical analysis is required to show that these samples cannot be considered as arising from the same population. If inspection of the figure itself is not sufficiently convincing, a very simple test suffices to show that the probability of the two samples arising by random sampling from a single population is very small, regardless of whether or not the growth law on the basis of which the regressions were calculated is exactly correct. Under the hypothesis that the Costa Rican sample was drawn from the same population as the Hawaiian sample, we should expect the points for Costa Rican fish to be half the time above and half the time below the corresponding values predicted from the Hawaiian sample. For each size class, the Costa Rican value falls below the value which would be expected on the basis of the Hawaiian sample. The probability of this occurring by chance alone for all 10 Costa Rican points is $(\frac{1}{2})^{10}$ or 1 chance in 1024; it is, then, most unlikely.

In figure 2 are plotted values of logarithm of length of second dorsal fin against logarithm of total length. This transformation yields a linear regression for the Costa Rican sample, the fish in which are from 54 cm. to 157 cm. in total length. Similarly, the Hawaiian data for fish 62 cm. and over in total length are rather well fitted by a linear regression, as shown in the figure (we have no Hawaiian specimens between 54 cm. and 62 cm.). We have also plotted in the figure the second-degree polynomial that fits the Hawaiian data for all sizes of fish in our sample. It is obvious, whichever regression we employ for the Hawaiian fish, that the second dorsal fins of yellowfin tuna from waters of the Hawaiian Islands grow, relative to total length, faster than those of yellowfin tuna from waters off Costa Rica. The difference in fin lengths is small at smaller sizes of fish, but increases with size of fish until among large fish the difference is very striking.

As may be seen from figure 3, the same situation obtains for the length of anal fin relative to total length. As has been reported for Costa Rican fish and African fish, the variability of fin lengths of second dorsal and anal fins, even on a logarithmic scale, is not entirely independent of size of fish, but tends to be greater at larger sizes. For this reason the values of s for the corresponding equations in table 2 and on page 359 are average values, and will be a little too small at large fish sizes and too large at small sizes.

Comparison of the linear regressions of figures 2 and 3 may be made by means of analysis of covariance (Kendall 1946, p. 237 *et seq.*); or, without reference to regression equations, we may simply compare the mean values of the several size classes and, following the same sort of reasoning as above in the case of the pectoral fin, arrive at the conclusion that the probability of the samples being drawn from a single population is very small.

The first dorsal spine was the longest on each of the 188 specimens for which this character was measured. As noted on page 359, a linear regression did not provide a good fit to the original data, compared with a linear regression fitted to the logarithms of the variables. The latter is plotted in figure 4. It was found that the same transformation applied to the Costa Rican data, yielded a linear regression with a slightly improved fit to those data also (Schaefer 1948 fitted a linear regression to the original data); this regression also is plotted in figure 4. Analysis of covariance shows that the slopes of the two regressions do not differ more than might be expected by chance, but the levels do; the longest dorsal spines of Hawaiian fish appear on the average to be a small, constant percentage shorter than the longest dorsal spines of Costa Rican fish.

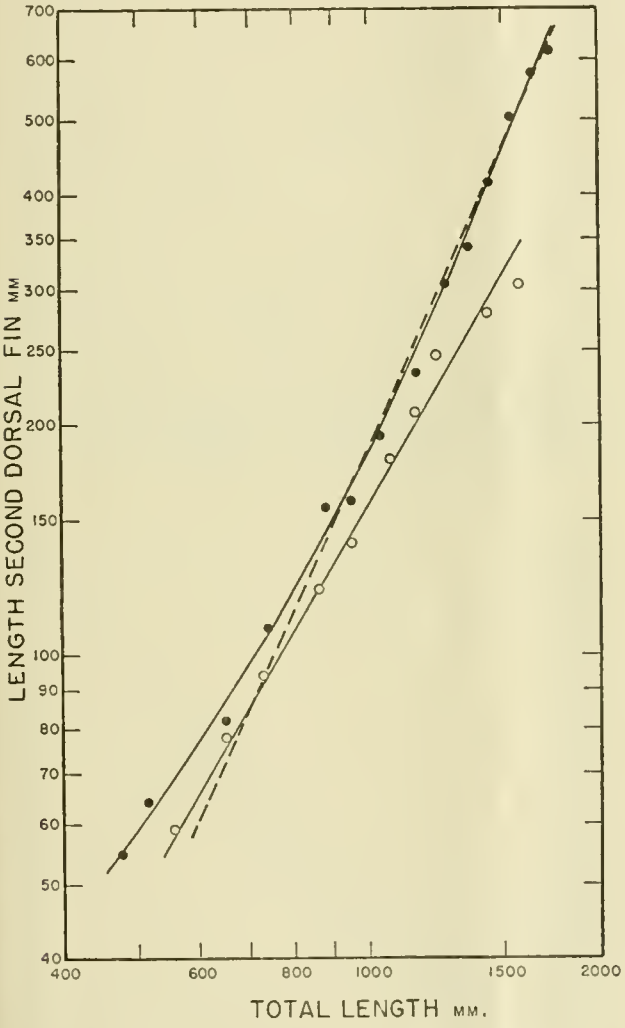

FIGURE 2.—Relations between length of second dorsal fin and total length. Open circles represent Costa Rican data; solid circles represent Hawaiian data. Solid straight line is linear regression line fitted to Costa Rican data. Broken straight line is linear regression line fitted to Hawaiian data from fish 600 mm. and over in total length. Solid curved line is second degree polynomial fitted to all Hawaiian data.

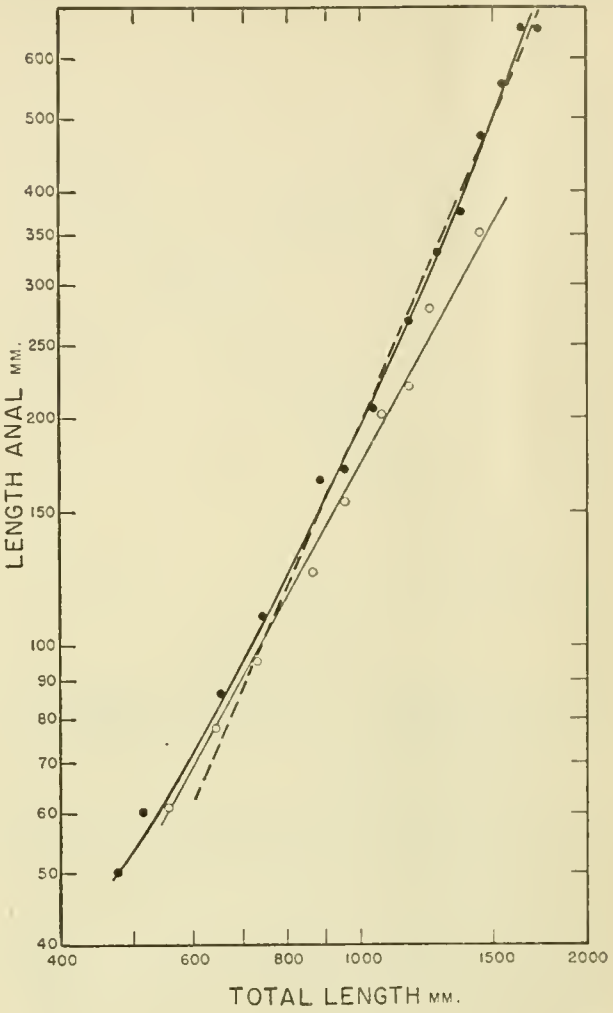

FIGURE 3.—Relations between length of anal fin and total length. Open circles represent Costa Rican data; solid circles represent Hawaiian data. Solid straight line is linear regression line fitted to Costa Rican data. Broken straight line is linear regression line fitted to Hawaiian data from fish 600 mm. and over in total length. Solid curved line is second degree polynomial fitted to all Hawaiian data.

Similarly, the logarithms of length of longest dorsal finlet against logarithm of total length yielded a linear regression for the Hawaiian measurements on all sizes of fish, and proved also to provide a good fit to the Costa Rican data for

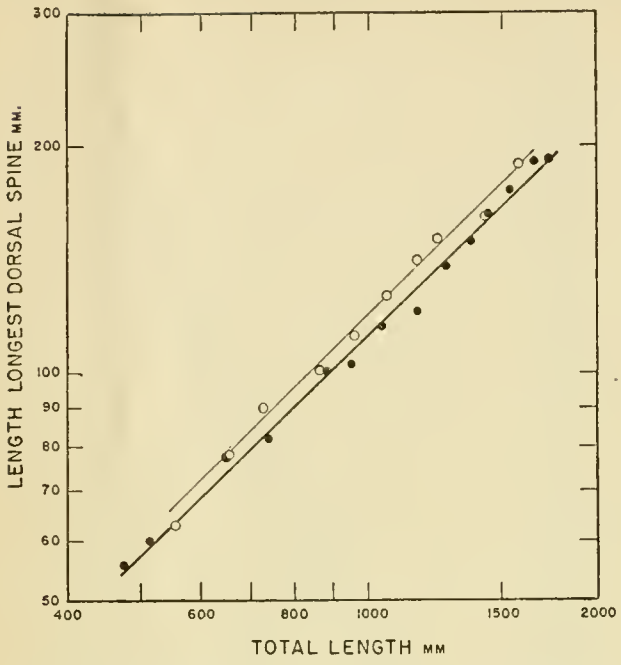

FIGURE 4.—Relations between length of longest dorsal spine and total length. Open circles and fine line represent Costa Rican data; solid circles and heavy line represent Hawaiian data.

which Schaefer (1948) had fitted a linear regression to the original data. Again, the resulting regressions, plotted in figure 5, when subjected to covariance analysis, indicate a small, constant average percentage difference between finlet lengths of the two populations, the Hawaiian fish having the longer finlets.

Head length and distances from snout to fin insertions

As mentioned earlier, Godsil (1948) has published the measurements of total length, head length, and distances from tip of snout to the insertions of first dorsal, second dorsal, anal, and ventral fins for nearly 2,000 specimens of yellowfin tuna from the American west coast between Cape San Lucas and Panama. The original measurements were published with his analyses of them, so we are able to compare these extensive data both with the Costa Rican data published by Schaefer (1948) and with the Hawaiian data presented herein. In figures 6 to 10 have been plotted head length and distances from snout to fin insertions against total length, which is taken in each case as the independent variable. For each of the three groups of data (Godsil's, Costa Rican, Hawaiian) have been plotted the mean values of the two variables in each graph for each 10 cm. of total length. To the pooled west-coast data (Godsil's plus my Costa Rican) have been fitted and plotted linear regressions. Also plotted are the curvilinear regressions computed by Godsil (1948, p. 13) for his data, of the type $y=a+bx+c/x$. On the same graphs have been plotted also the linear-regression line best fitting the Hawaiian data and the best-fitting curvilinear regression of the type selected by Godsil.

For the Hawaiian data, except in one case (snout to insertion of second dorsal of Hawaiian fish), the curvilinear regressions provide a slight improvement in fit over the linear regressions. Inspection of the figures, however, reveals that the differences between the linear and curvilinear regressions are small in comparison with the differences between west-coast and Hawaiian samples. The reduction of the variance about the regression line also is very small in comparison with the difference between the two regions when a curvilinear rather than a linear equation is employed. In consequence, the linear-regression equations will be employed below in considering the application of analysis of covariance to the comparison of samples.

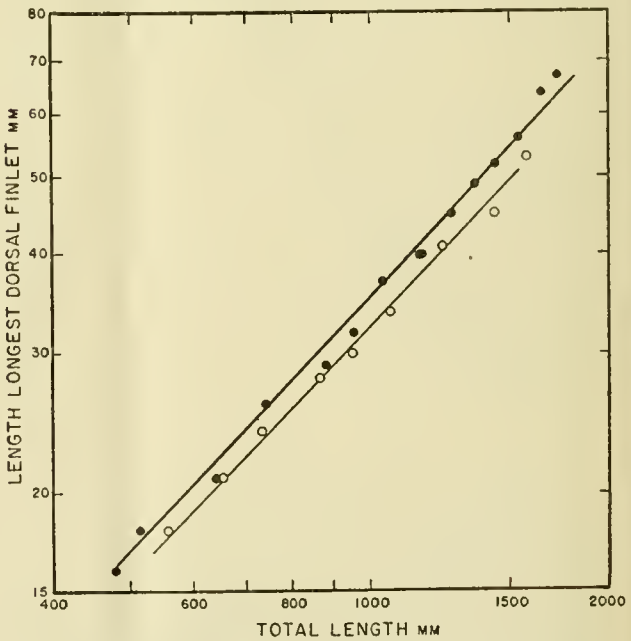

FIGURE 5.—Relations between length of longest dorsal finlet and total length. Open circles and fine line represent Costa Rican data; solid circles and heavy line represent Hawaiian data.

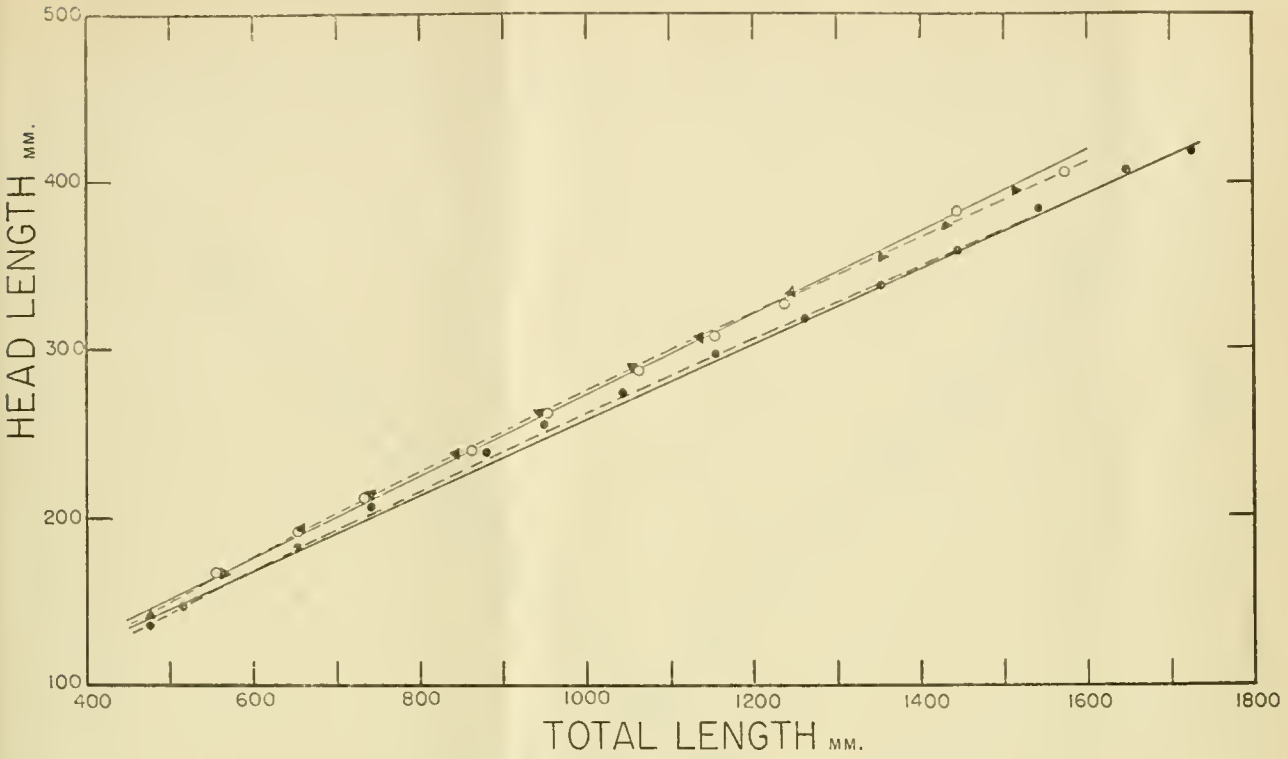

FIGURE 6.—Relations between head length and total length. Solid circles represent Hawaiian data; open circles represent Costa Rican data; solid triangles represent Godsil's west-coast data. Fine solid line is linear regression line fitting west-coast data, while heavy solid line is linear regression line fitting Hawaiian data. Fine broken line is Godsil's curvilinear regression for west-coast data, while heavy broken line is similar regression fitted to Hawaiian data.

A detailed analysis of covariance is not necessary to arrive at the conclusion that with respect to these dimensions the samples from the Hawaiian Islands are different from the samples from the west coast. It is quite obvious from the plots of the mean values for each 10-cm. size class (figs. 6 to 10) that the head length and the distances from snout to the fin insertions are significantly shorter for Hawaiian than for west-coast yellowfin tuna at the larger sizes. If a statement of probability is desired to test a null hypothesis respecting difference between regions, one may proceed in a manner similar to that suggested above in the case of pectoral-fin lengths, confining attention for sake of simplicity to the larger sizes of tuna, say over 800 mm. in total length.

Considering fish of size classes between 800 mm. and 1,600 mm. in total length, for which specimens were available both from the west coast and from Hawaii, the points for the mean values of each 10-cm. length class of Hawaiian fish fall below the values expected on the basis of west-coast data in all cases for head length (fig. 6), snout to insertion of anal (fig. 7), snout to insertion of second dorsal (fig. 8), and snout to insertion of ventral (fig. 9). Since there are 8 such points for each dimension, and under a null hypothesis they might equally well be above or below the value expected from west-coast data, the probability of the observations on the hypothesis is $(\frac{1}{2})^8=\frac{1}{256}$ for each dimension, which is unlikely. For snout to insertion of first dorsal, one point (900-mm. size class) falls barely above the expected value; the probability of having at most one point above the expected value under the null hypothesis is $(\frac{1}{2})^8+8(\frac{1}{2})^8=\frac{9}{256}$.

By the conventional methods of analysis of covariance (Kendall 1946, p. 237 *et seq.*), we may also test for each of the dimensions the null hypotheses (1) that the sample from the west coast and the sample from Hawaii may both be represented by a single linear-regression equation

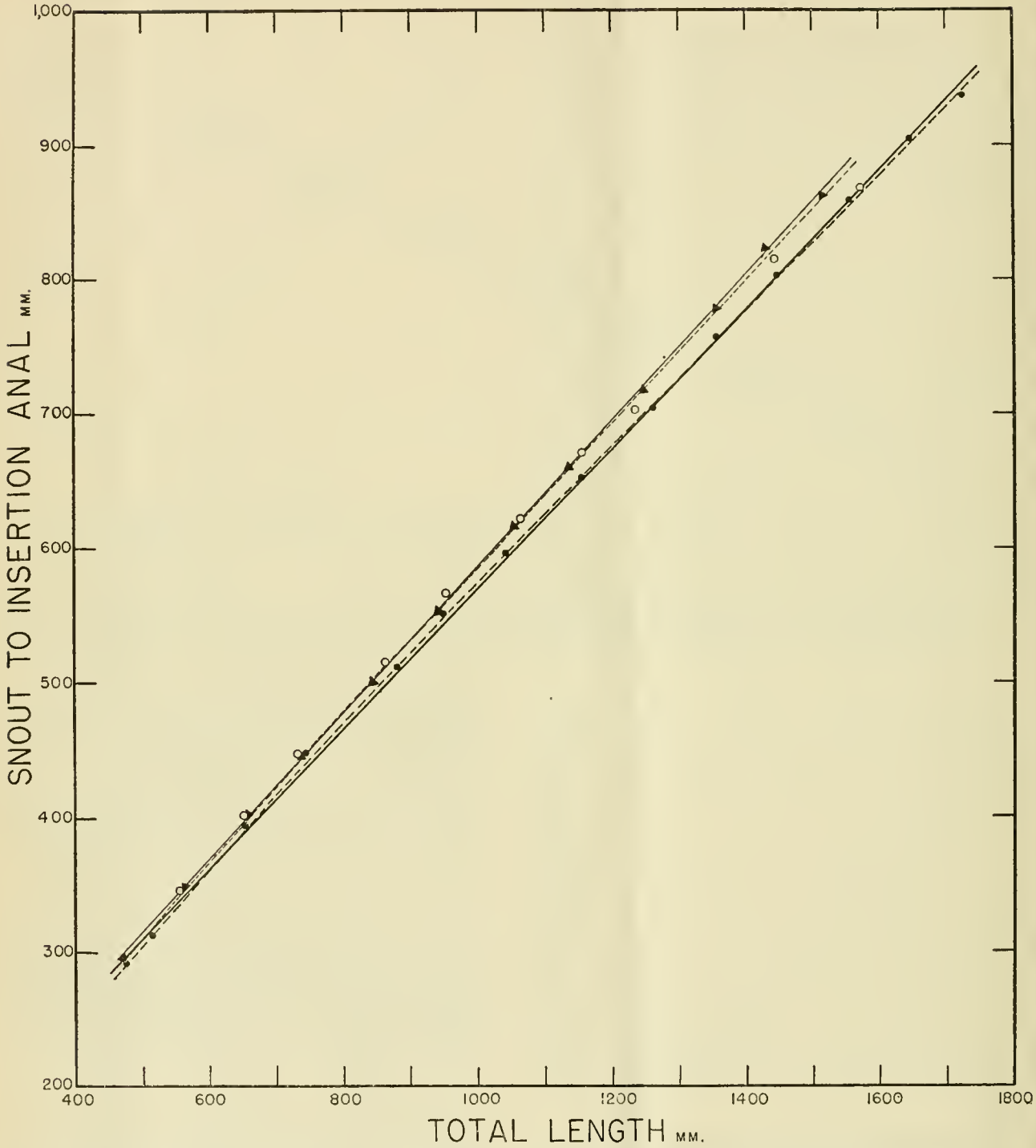

FIGURE 7.—Relations between distance from snout to insertion of anal fin and total length. Solid circles represent Hawaiian data; open circles represent Costa Rican data; solid triangles represent Godsil's west-coast data. Fine solid line is linear regression line fitting west-coast data, while heavy solid line is linear regression line fitting Hawaiian data. Fine broken line is Godsil's curvilinear regression for west-coast data, while heavy broken line is similar regression fitted to Hawaiian data.

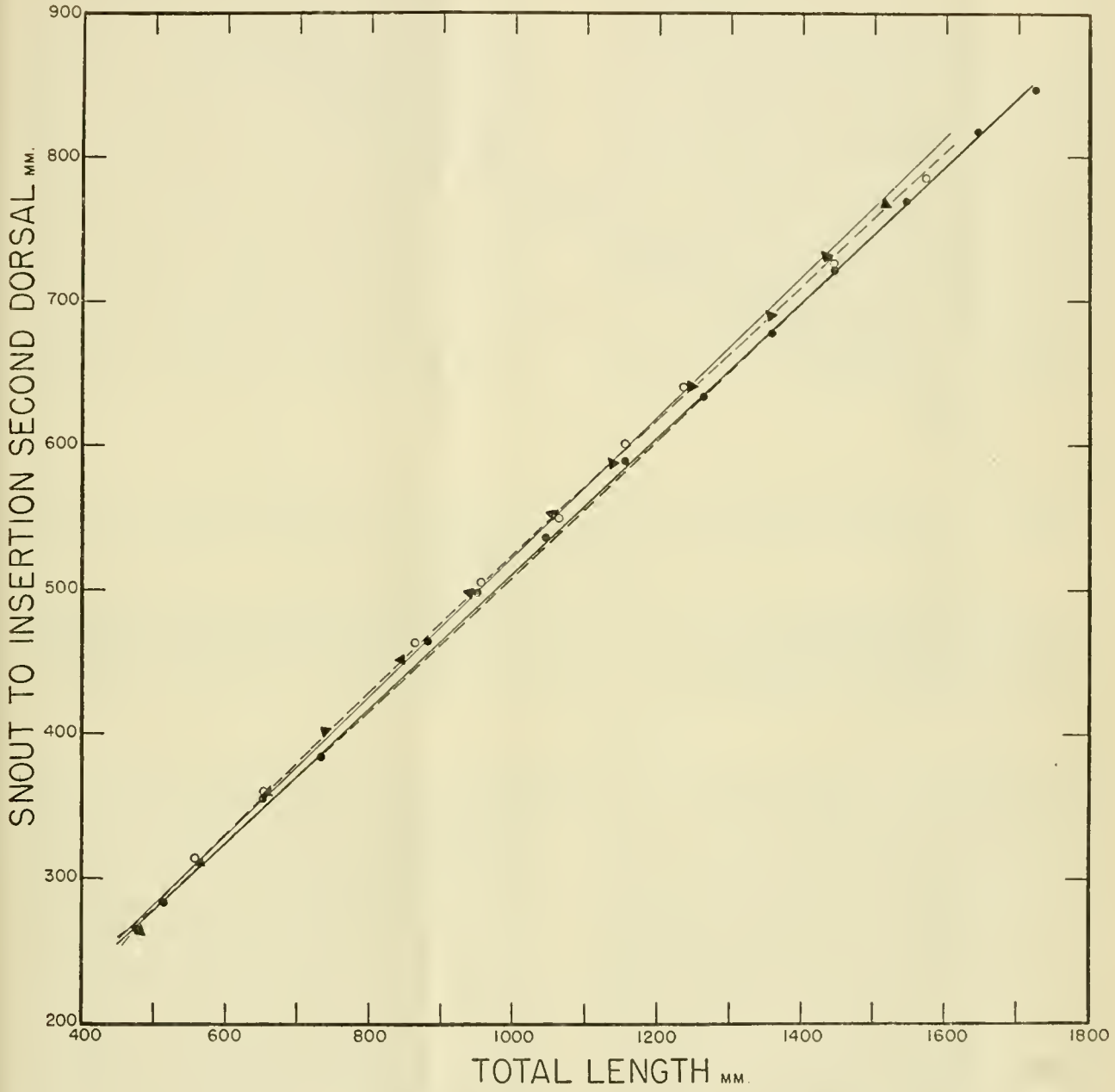

FIGURE 8.—Relations between distance from snout to insertion of second dorsal fin and total length. Solid circles represent Hawaiian data; open circles represent Costa Rican data; solid triangles represent Godsil's west-coast data. Fine solid line is linear regression line fitting west-coast data, while heavy solid line is linear regression line fitting Hawaiian data. Fine broken line is Godsil's curvilinear regression for west-coast data, while heavy broken line is similar regression fitted to Hawaiian data.

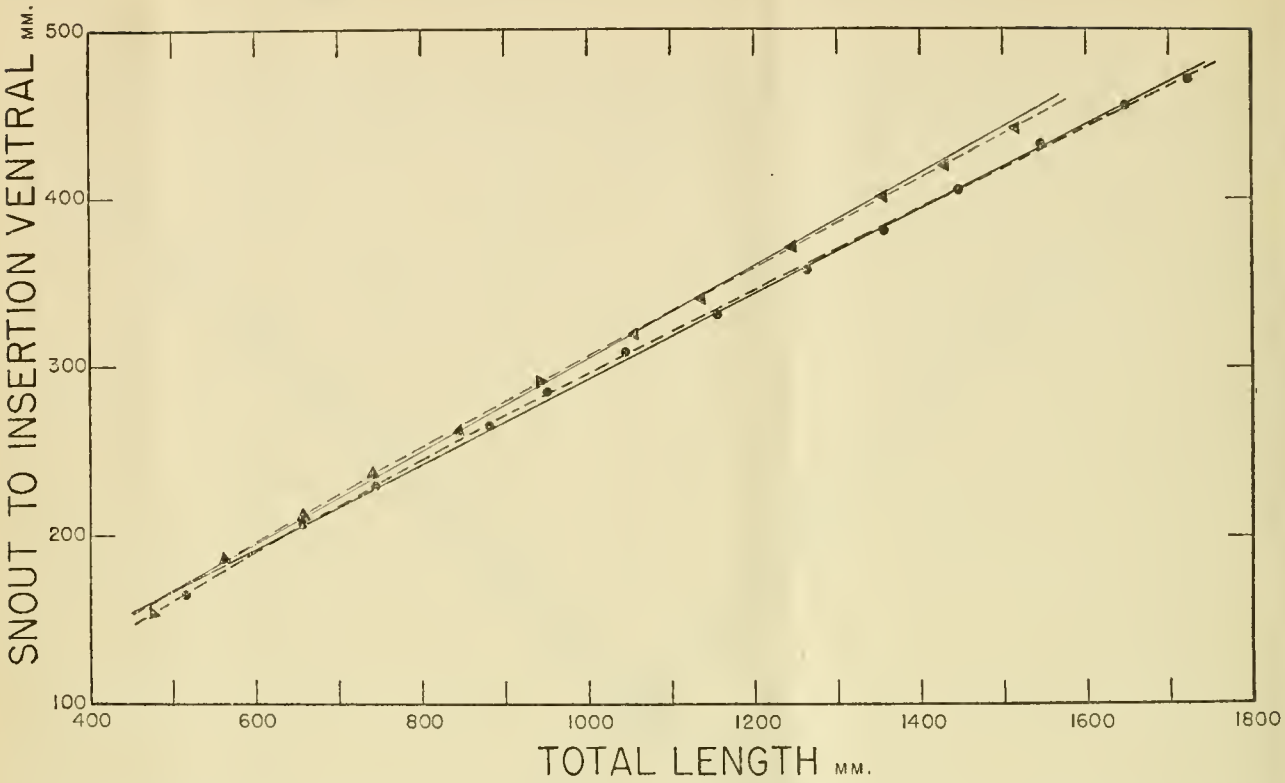

FIGURE 9.—Relations between distance from snout to insertion of ventral fin and total length. Solid circles represent Hawaiian data; open circles represent Costa Rican data; solid triangles represent Godsil's west-coast data. Fine solid line is linear regression line fitting west-coast data, while heavy solid line is linear regression line fitting Hawaiian data. Fine broken line is Godsil's curvilinear regression for west-coast data, while heavy broken line is similar regression fitted to Hawaiian data.

and, if this be false, (2) that the regression coefficients (slopes) of the regression lines fitting the samples from the two regions are equal. As may be seen from the variance ratios computed in table 3, both these hypotheses are to be rejected for each dimension considered, the west-coast data in this table including the measurements of both Schaefer and Godsil. If we compare the Hawaiian data with the data of Schaefer alone (table 4) we find here also that for no character considered may the data from the two regions be represented by a single linear-regression equation. In two cases, however, indicated by footnotes in the table, the appropriate variance ratio indicates that there is not sufficient reason from these particular data to reject the hypothesis of equality of regression coefficients. In general, it is quite apparent that for each character the regression lines are different for the two regions and that they differ in slope.

Comparison of the regression lines of the dimensions of tuna from different regions is perfectly straightforward so long as we are able to assume that the sample regression lines are representative of the tuna populations of the regions in each case. As has been noted earlier, however, Godsil found that repeated samples from the west coast yielded regression lines (curvilinear) for which a null hypothesis could not be supported. The same thing is true if linear regressions are applied to his data (table 5). His various subgroups along the west coast differ significantly among themselves, and for each dimension they differ in respect of the regression coefficients. As may be seen from table 6, comparison of my Costa Rican data with Godsil's data from Costa Rica alone (his samples 4, 5, and 12) reveals that a single linear-regression

equation does not, for any dimension, accurately describe both. It is quite evident that differences may be expected among different samples from the same region. The problem, then, is to determine whether the differences between regions are greater than might reasonably be expected among different samples from the same region. In comparing Hawaiian and west-coast data, where the differences are so large that the distributions of means of subclasses (size groups) are completely separate between the two regions for the most part, the answer is fairly obvious from the graphs of the type herein presented. In table 7 have been tabulated the linear-regression coefficients for each of Godsil's 13 samples, for my Costa Rican sample, and for the Hawaiian sample. From this tabulation it may readily be seen that the Hawaiian regression coefficients fall, for each dimension, well below the lowest value encountered among the several west-coast subsamples.

Although in the case at hand we are spared the need for an efficient means of comparing variation between samples within a region with differences between regions where a null hypothesis is not valid for samples within the region, this will not in general be true. The desirability of a test for application in other, less-clear situations is sufficiently great that some examination of the problem seems warranted, particularly in view of the fact that Godsil (1948) has already attempted to develop and employ such a test. We wish, therefore, to consider the problem of measuring the differences between groups where a null hypothesis is not satisfied.

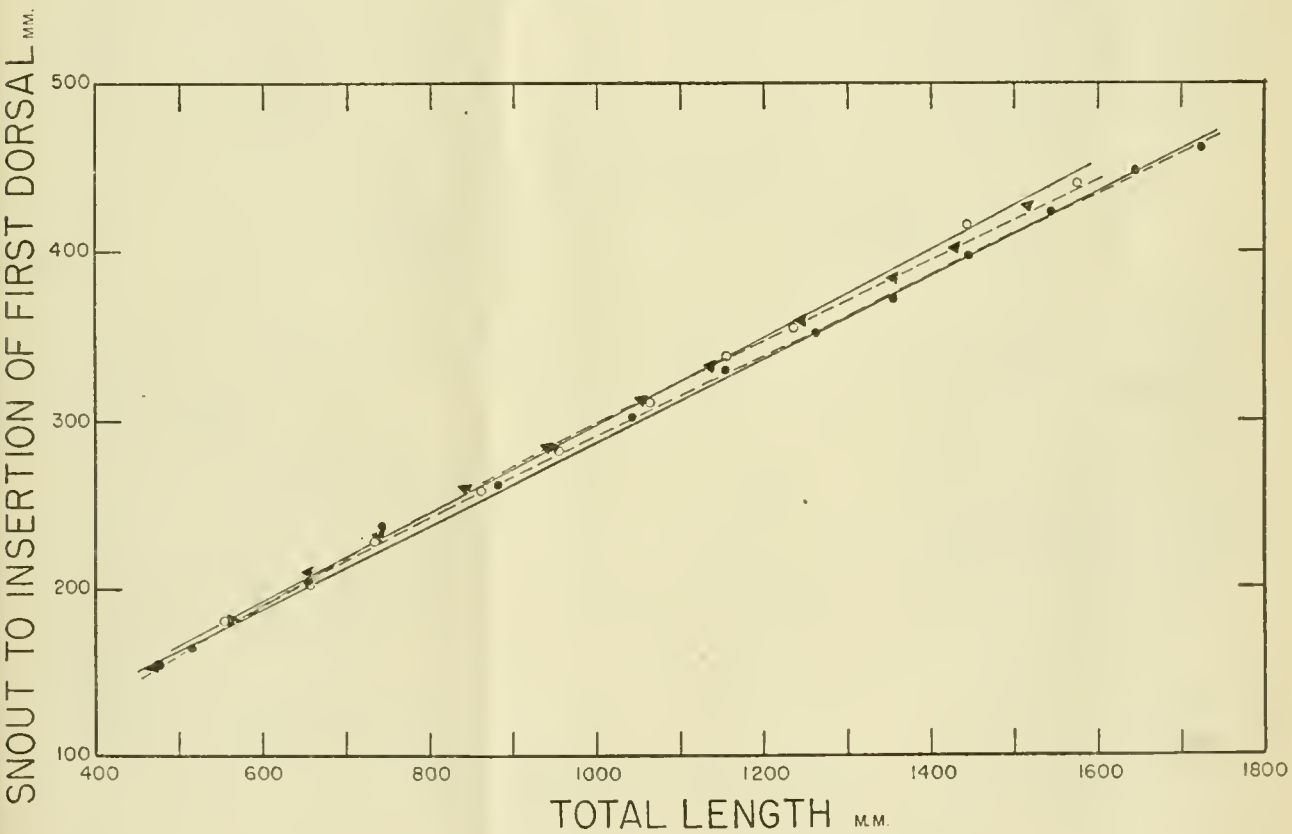

FIGURE 10.—Relations between distance from snout to insertion of first dorsal fin and total length. Solid circles represent Hawaiian data; open circles represent Costa Rican data; solid triangles represent Godsil's west-coast data. Fine solid line is linear regression line fitting west-coast data, while heavy solid line is linear regression line fitting Hawaiian data. Fine broken line is Godsil's curvilinear regression for west-coast data, while heavy broken line is similar regression fitted to Hawaiian data.

TABLE 3.—*Comparison of Hawaiian data and pooled American west-coast data by covariance analysis, linear regressions*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratios
Head length:				
Deviations from total regression	2, 158	73, 920		$\frac{20,611}{15.17}=1359.0$
Deviations from regressions within regions	2, 156	32, 698	15. 17	
Differences between regions	2	41, 222	26, 611	$\frac{6,257}{15.17}=412.5$
Differences between regression coefficients	1	6, 257	6, 257	
Differences between adjusted means	1	34, 965		
Snout to insertion first dorsal:				
Deviations from total regression	2, 156	67, 803		$\frac{8,188}{23.88}=342.9$
Deviations from regressions within regions	2, 154	51, 427	23. 88	
Differences between regions	2	16, 376	8, 188	$\frac{3,431}{23.88}=143.7$
Differences between regression coefficients	1	3, 431	3, 431	
Differences between adjusted means	1	12, 945		
Snout to insertion ventral:				
Deviations from total regression	2, 110	87, 708		$\frac{17,881}{24.64}=725.7$
Deviations from regressions within regions	2, 108	51, 946	24. 64	
Differences between regions	2	35, 762	17, 881	$\frac{7,709}{24.64}=312.9$
Differences between regression coefficients	1	7, 709	7, 709	
Differences between adjusted means	1	28, 053		
Snout to insertion second dorsal:				
Deviations from total regression	2, 156	102, 228		$\frac{12,232}{36.10}=338.8$
Deviations from regressions within regions	2, 154	77, 765	36. 10	
Differences between regions	2	24, 463	12, 232	$\frac{4,263}{36.10}=118.1$
Differences between regression coefficients	1	4, 263	4, 263	
Differences between adjusted means	1	20, 200		
Snout to insertion anal:				
Deviations from total regression	2, 153	128, 518		$\frac{26,355}{35.24}=747.9$
Deviations from regressions within regions	2, 151	75, 808	35. 24	
Differences between regions	2	52, 710	26, 355	$\frac{12,017}{35.24}=341.0$
Differences between regression coefficients	1	12, 017	12, 017	
Differences between adjusted means	1	40, 693		

TABLE 4.—*Comparisons of Hawaiian data and Schaefer's Costa Rican data by covariance analysis, linear regressions*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratios
Head length:				
Deviations from total regression	241	10, 649		$\frac{625}{39.33}=15.89$
Deviations from regressions within regions	239	9, 399	39. 33	
Differences between regions	2	1, 250	625	$\frac{143}{39.33}=$[1] 3.64
Differences between regression coefficients	1	143	143	
Differences between adjusted means	1	1, 107	1, 107	$\frac{1,107}{39.76}=27.84$
Snout to insertion first dorsal:				
Deviations from total regression	245	16, 558		$\frac{1,004}{59.88}=16.77$
Deviations from regressions within regions	243	14, 550	59. 88	
Differences between regions	2	2, 008	1, 004	$\frac{552}{59.88}=9.22$
Differences between regression coefficients	1	552	552	
Differences between adjusted means	1	1, 456		
Snout to insertion second dorsal:				
Deviations from total regression	246	35, 349		$\frac{2,626}{123.35}=21.29$
Deviations from regression within regions	244	30, 097	123. 35	
Differences between regions	2	5, 252	2, 626	$\frac{164}{123.35}=$[1] 1.33
Differences between regression coefficients	1	164	164	
Differences between adjusted means	1	5, 088	5, 088	$\frac{6,088}{123.51}=41.20$
Snout to insertion anal:				
Deviations from total regression	246	36, 130		$\frac{6,460}{95.12}=67.91$
Deviations from regression within regions	244	23, 210	95. 12	
Differences between regions	2	12, 920	6, 460	$\frac{536}{95.12}=5.63$
Differences between regression coefficients	1	536	536	
Differences between adjusted means	1	12, 384		

[1] Not significant.

TABLE 5.—*Comparison of subgroups, Godsil's west-coast data, by covariance analysis, linear regressions*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratios
Head length:				
Deviations from total regression	1,909	23,049		$\frac{198.1}{9.705}=20.41$
Deviations from regression within groups	1,885	18,294	9.705	
Differences among groups	24	4,755	198.1	$\frac{147.8}{9.705}=15.23$
Differences among regression coefficients	12	1,773	147.8	
Differences among adjusted group means	12	2,982		
Snout to insertion first dorsal:				
Deviations from total regression	1,909	36,411		$\frac{199.5}{16.78}=11.89$
Deviations from regression within groups	1,885	31,623	16.78	
Differences among groups	24	4,788	199.5	$\frac{187.3}{16.78}=11.17$
Differences among regression coefficients	12	2,248	187.3	
Differences among adjusted group means	12	2,540		
Snout to insertion ventral:				
Deviations from total regression	1,907	37,960		$\frac{112.1}{18.73}=5.99$
Deviations from regression within groups	1,883	35,269	18.73	
Differences among groups	24	2,691	112.1	$\frac{49.25}{18.73}=2.63$
Differences among regression coefficients	12	591	49.25	
Differences among adjusted group means	12	2,100		
Snout to insertion second dorsal:				
Deviations from total regression	1,908	47,560		$\frac{278.7}{21.69}=12.85$
Deviations from regression within groups	1,884	40,871	21.69	
Differences among groups	24	6,689	278.7	$\frac{364.9}{21.69}=16.82$
Differences among regression coefficients	12	4,379	364.9	
Differences among adjusted group means	12	2,310		
Snout to insertion anal:				
Deviations from total regression	1,905	51,914		$\frac{387.5}{22.65}=17.11$
Deviations from regression within groups	1,881	42,615	22.65	
Differences among groups	24	9,299	387.5	$\frac{228.8}{22.65}=10.10$
Differences among regression coefficients	12	2,745	228.8	
Differences among adjusted group means	12	6,554		

TABLE 6.—*Comparisons of Schaefer's and Godsil's Costa Rican data by covariance analysis, linear regressions*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratios
Head length:				
Deviations from total regression	808	10,018		$\frac{144}{12.07}=11.93$
Deviations from regression within groups	806	9,730	12.07	
Differences between groups	2	288	144	$\frac{83}{12.07}=6.88$
Differences between regression coefficients	1	83	83	
Differences between adjusted group means	1	205	205	
Snout to insertion first dorsal:				
Deviations from total regression	808	16,550		$\frac{142}{20.18}=7.04$
Deviations from regression within groups	806	16,226	20.18	
Differences between groups	2	284	142	$\frac{120}{20.18}=5.95$
Differences between regression coefficients	1	120	120	
Differences between adjusted group means	1	164	164	
Snout to insertion second dorsal:				
Deviations from total regression	807	27,293		$\frac{65.5}{33.74}=[1]2.00$
Deviations from regression within groups	805	27,162	33.74	
Differences between groups	2	131	65.5	
Differences between regression coefficients	1	60	60	
Differences between adjusted group means	1	71	71	
Snout to insertion anal:				
Deviations from total regression	806	23,849		$\frac{218}{29.12}=7.49$
Deviations from regression within groups	804	23,412	29.12	
Differences between groups	2	437	218	$\frac{52}{29.12}=[1]1.79$
Differences between regression coefficients	1	52	52	
Differences between adjusted group means	1	385	385	$\frac{385}{29.15}=13.21$

[1] Not significant.

Denote by x_{ij}, y_{ij} the pair of variate values for the i^{th} member of the j^{th} group, by n_j the number of members of the j^{th} group, and by p the number of groups. Also let $x_{.j}$ and $y_{.j}$ be the mean values of the variates in the j^{th} group, $x..$ and $y..$ be the mean values of the variates for the total of all groups, and N be the total of all n_j. The variances about the linear-regression lines may be analyzed as follows:

Variation	Degrees of freedom	Sum of squares	Mean square
Total, from regression b_0	$N-2$	$S=\sum_{i,j}(y_{ij}-y..)^2-b_0\sum_{i,j}(x_{ij}-x..)(y_{ij}-y..)$	$S/N-2$
Within groups, from regression b_j	$N-2p$	$S_2=\sum_{i,j}(y_{ij}-y_{.j})^2-\sum_{i,j}b_j(x_{ij}-x_{.j})(y_{ij}-y_{.j})$	$S_2/N-2p=s_2$
Differences between groups	$2p-2$	$S_1=\sum_j n_j(y_{.j}-y..)^2-b_0\sum_j n_j(x_{.j}-x..)(y_{.j}-y..)$ $-\sum_{i,j}(b_0-b_j)(x_{ij}-x_{.j})(y_{ij}-y_{.j})$	$S_1/2p-2=s_1$

TABLE 7.—*Regression coefficients for regressions of various dimensions on total length, for samples from the American west coast and Hawaii*

	Head length	Snout to insertion first dorsal	Snout to insertion ventral	Snout to insertion second dorsal	Snout to insertion anal
Godsil's west-coast samples:					
No. 1	0.24315	0.27134	0.26520	0.50285	0.54569
No. 2	.27902	.29256	.29840	.49022	.55697
No. 3	.24339	.26627	.27189	.48265	.53736
No. 4 [1]	.23771	.25647	.27185	.47464	.53656
No. 5 [1]	.24118	.25793	.27210	.48137	.54344
No. 6	.26280	.28873	.29487	.52624	.57669
No. 7	.23740	.25746	.27615	.47767	.54490
No. 8	.25580	.28390	.27536	.50448	.55711
No. 9	.26001	.28341	.28676	.50524	.54416
No. 10	.26014	.28015	.29405	.50883	.58550
No. 11	.23811	.26397	.27348	.49191	.54836
No. 12 [1]	.28004	.30858	.30067	.50391	.55914
No. 13	.25999	.28519	.28528	.50207	.58009
All samples	.24356	.26148	.27244	.48358	.54383
Schaefer's Costa Rican samples	.23504	.26346	.....	.47675	.53508
Hawaiian samples	.22567	.24821	.25259	.46914	.51941

[1] Samples from Costa Rican waters.

Where b_o is the regression coefficient for all data pooled and b_j is the regression coefficient for the j^{th} group.

When the null hypothesis is satisfied s_1 and s_2 are both unbiased estimates of the variance about the regression line, and their ratio will be distributed in the F distribution.

In the case where the null hypothesis is not satisfied, but a single regression coefficient adequately describes the effect of x on y for all groups, we may subtract

$$Y_{ij}=y..+b_o(x_{ij}-x..)$$

from each value of y_{ij} to allow for differences in the x variate. The new variable $y'_{ij}=y_{ij}-Y_{ij}$ is completely corrected for variations in x, so that differences between adjusted means of groups will be independent of the values of x. We may take, then, an estimate of the differences among the adjusted group means as a measure of the differences between groups which will not be affected by differences in size composition (values of x) of the samples from the different groups (Kendall 1946, p. 244). Geometrically, in this case, the lines are parallel, so that the distance between lines is constant for all values of x.

In the case where a single regression coefficient does *not* represent the effect of x on y for all groups, geometrically where the lines are not parallel, any measurement of the distance between lines will depend on the value or values of x employed for the measurement of the distance. Differences between corrected group means will, then, not be independent of the x values. Geometrically, the distances between regression lines will be dependent upon the selection of the place where the distances are measured. In this situation, obviously, differences between adjusted group means are of small value in measuring differences between groups, when the values of x are selected arbitrarily.

Godsil's statistic (Godsil 1948, p. 9, table 4), the mean-square deviation of the sample regression line of the group from the sample regression line of all data pooled, based on curvilinear regressions, is similarly dependent on the distribution of the x values of the variates composing the groups, since the regression coefficients are not equal (the lines are not parallel). Its employment as a standard for judging differences between regions as compared with differences among groups within the region is, therefore, subject to strong objection.

It seems, then, that where the groups within a region differ in their regression coefficients, as is true in the present instance, we have no method of measuring with any precision the differences among these groups as a basis of judging whether a further sample from another region could reasonably be expected to belong to the same population as that from which the groups in question were drawn. Of course, in the event the regression coefficient itself is not size-connected, it may be used to characterize the group, and one might compare the variation among group regression coefficients with the observed value of the regression coefficient from the further sample from another region (e. g. table 7).

Pending development of a method of precise analysis, comparison of differences among regression lines within regions with differences between regions does not appear to be very fruitful, except in those cases where the difference between regions is so very much greater than differences among samples within a region that it is quite apparent from a simple graph of the data and no precise method of analysis is required.

As a practical procedure it appears best, perhaps, to select fish from each region from many different schools, and of sizes that will cover the entire range available, and then, in comparing data between regions by covariance analyses, to compare samples of similar size range. In this manner any variation between groups within the region will tend to be assimilated into the variance of the total sample for the whole region, and the total sample will be nearly representative of the population of the region.

Other dimensions

Comparison of the regression of diameter of iris on head length of Hawaiian specimens with that of Costa Rican specimens indicates that the relation is different in the two regions. The relations and the means of the two variates for each 10 centimeters of total length are plotted in figure 11.

Comparison of Hawaiian and Costa Rican data respecting regressions of length of maxillary on head length, body depth on total length, and weight on total length indicated that in each case the two samples might have been drawn at random from a single population so far as these characters are concerned.

Counts of gill rakers

Counts of total gill rakers of 188 Hawaiian tuna (table 1) have a mean value of 29.66 with a standard error of .0870. Schaefer's (1948) Costa Rican data on 45 specimens have a mean value of 30.60 with a standard error of .186, while Godsil and Byer's (1944) counts of 60 American-west-coast specimens have a mean of 30.35 with a standard error of .146. Comparison of the Costa Rican and Godsil and Byer's data yields a t value of 1.06, so that the null hypothesis is reasonable and we may pool these data to estimate the mean gill-raker count of yellowfin from the American west coast as 30.46 with a standard error of .116. The difference of .80 between this value and the Hawaiian mean is associated with a t value of 5.52.

We have verified from our Hawaiian data that there is no correlation between size of fish and gill-raker count. This character seems to offer good possibilities for racial analysis of tunas for that reason, since it will avoid the difficulties in comparisons which plagued us in regression analyses.

DISCUSSION

Hawaiian yellowfin tuna differ from those of the American west coast in having, on the average, longer pectoral fins at the same fish size, and this difference is greater for the larger fish. The same is true of the second dorsal and anal fins, but in these cases the fins of the Hawaiian fish also grow at an accelerated rate compared to west-coast fish, so that the difference in fin lengths among the largest fish sizes is very striking. The first dorsal spine appears to be consistently shorter among Hawaiian fish, while the longest dorsal finlet is longer.

Among Hawaiian fish, the distance from tip of snout to the posterior edge of the opercle and to the various fin insertions increases, relative to total length, more slowly than among west-coast fish so that all these dimensions are shorter, on the average, for the large fish from Hawaii than for west-coast fish of comparable size. From this it is evident that the posterior part of the trunk grows faster among Hawaiian fish so that at large sizes, say above 700 or 800 mm., the posterior part of the body is more elongate than among west-coast fish of similar sizes.

On the basis of the magnitude and consistency of these differences between the biometric charac-

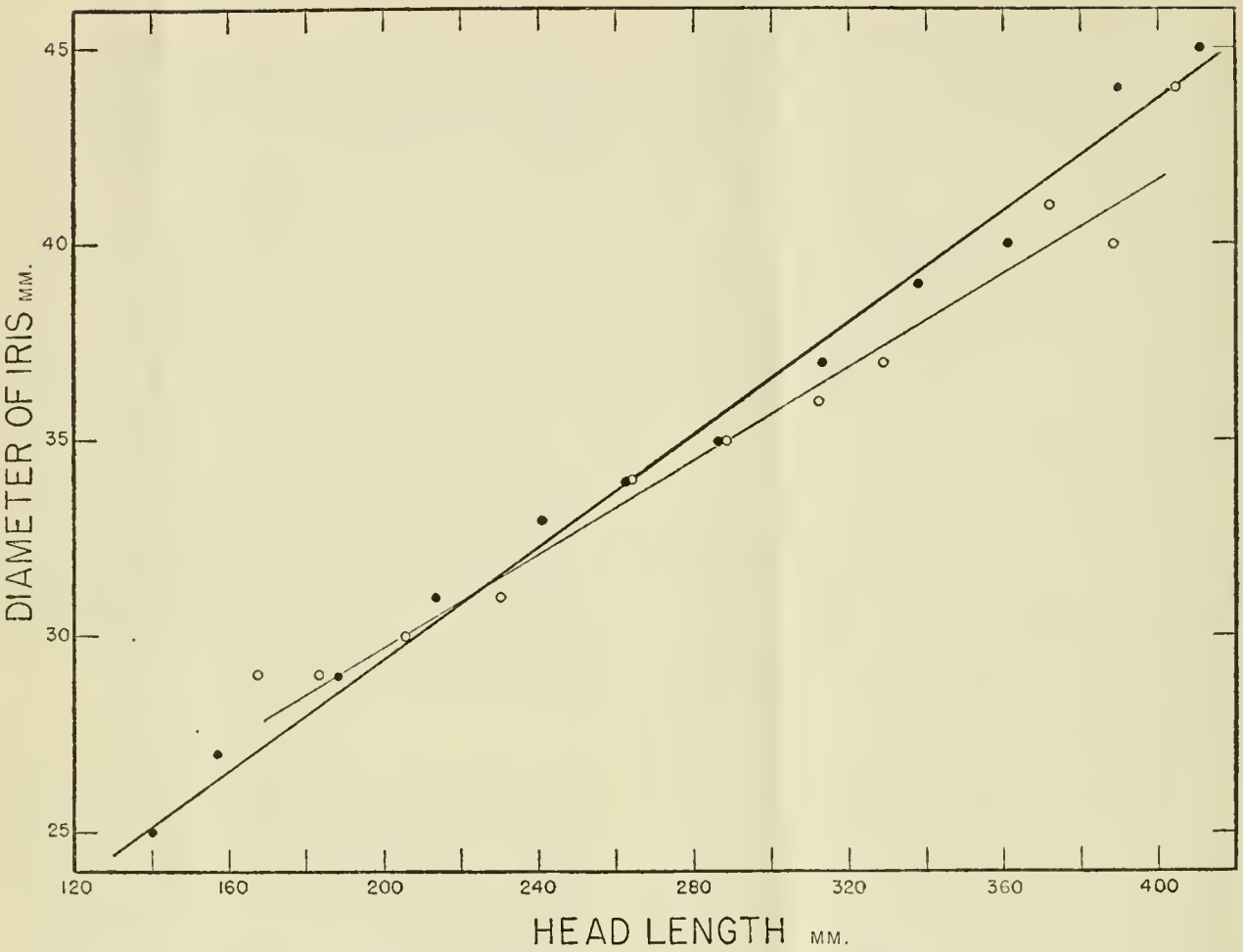

FIGURE 11.—Relations between diameter of iris and length of head. Open circles and fine line represent Costa Rican data; solid circles and heavy line represent Hawaiian data.

teristics of yellowfin tuna from the Hawaiian Islands and from the American west coast, there is no doubt that these two populations are to be regarded as distinct. The possibility of some mixing between them is not excluded, but if any exists it must be sufficiently small to permit the two populations to maintain their characteristic differences.

The statistical comparison of body-proportion data on tunas from different regions by regression analysis is beset with difficulties which are beyond the scope of this paper to deal with, and which seem not to be critical in this instance where the differences dealt with are of sufficient magnitude that sensitive methods are not required. The problem merits, however, further attention since it will become acute where differences to be measured are small.

This problem may be avoided by employing denumerable characters which are not size-connected. Gill-raker counts seem to be a useful character of this sort. The Hawaiian and west-coast yellowfin-tuna populations are quite distinct with respect to mean gill-raker count.

The fact, brought out by this study, that the yellowfin tuna of the central Pacific belong to a population distinct from that along the American west coast, has important implications in the development and management of the tuna fisheries. Since the yellowfin tuna of these regions belong to different populations which do not freely intermix, a fishery on one can have no effect on the abundance of the other. The fishery along the west coast is not tapping the entire yellowfin-tuna resource of the Pacific.

The various biometric differences demonstrated herein are of about the same magnitude as the differences between yellowfin tuna from the waters of the American west coast and from the Atlantic off Africa (Schaefer and Walford 1950). In some cases, such as the lengths of second dorsal and anal fins, the differences between the two samples from the Pacific are even more striking than the differences between African and American west-coast samples. If it is borne out by further study that the variation within oceans is about as great as the variation between them, it will be necessary to regard all the yellowfin tunas as belonging to a single species. It is particularly desirable that a series of specimens be examined from the Indian Ocean, whence comes the type of *N. argentivittatus*, which has priority among the several descriptions of species of *Neothunnus*, in order to settle the question of nomenclature.

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FACTORS INFLUENCING THE ORIENTATION OF MIGRATING ANADROMOUS FISHES

By Gerald B. Collins

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CONTENTS

	Page
Historical background	375
Major theories on orientation	375
Sensory basis of orientation	376
Relation of sensory abilities to environmental patterns	376
Experimental approach	378
Materials and methods	378
Experimental method	379
Procedure	380
Controls	381
Water modification	382
Temperature	382
Gaseous content	382
Nongaseous chemicals	383
Measurements	383
Water samples	383
Titrations	384
Hydrogen-ion concentration	384
Alkalinity and HCO_3	384
Carbon dioxide	384
Oxygen	385
Temperature	385
Velocity	385
Aberrations in experimental control	385
Experiments	386
Orientative influence of temperature	386
Relation of temperature response to temperature level	387
Orientative influence of CO_2	387
Relative orientative influence of CO_2 and temperature	388
Orientative influence of pH	388
Experiments using nitrogen and oxygen	389
Nitrogen	389
Oxygen	389
Other factors influencing orientation	390
The 3:1 ratio of the response	391
Discussion	392
Summary	394
Literature cited	395

FACTORS INFLUENCING THE ORIENTATION OF MIGRATING ANADROMOUS FISHES

By Gerald B. Collins, *Fishery Research Biologist*

HISTORICAL BACKGROUND

The orientation of migrating fishes has been the subject of investigation and conjecture for many years. Migration paths have been outlined by tagging experiments, and a wealth of valuable information on the physiology, development, and behavior of migratory fishes has been acquired through the persistent efforts of many able investigators; but the means by which the fish are directed on their migrations are still largely a matter of speculation.

The purpose of the study presented here was to investigate the influence of certain physical and chemical factors upon the orientation of migrating anadromous fish of the genus *Pomolobus*. In the course of this investigation an effort was made to determine experimentally if the migrating fish would orient to differences in the physical and chemical characteristics of water.

The existence of differences in physical and chemical factors in natural waters to which fish might respond has long been known. Slight gradations usually exist in the relative amounts of dissolved gases, in *p*H, in temperature, and in other physical and chemical characteristics of a stream from the source to the mouth. Such gradients are usually so slight that the differences between points miles apart are still below the thresholds of the sensory perception of fish.

Much greater gradients are found at stream junctions and at stream entrances into lakes or into the sea. In these gradients there frequently are chemical and physical differences between points a few feet apart which are large enough to be detected by the fish. The existence of these gradients at crucial points along the migration paths of anadromous fishes where they might influence the fish in the selection of a stream has led to speculation on their possible role in directing the migration of the fish.

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MAJOR THEORIES ON ORIENTATION

Currently, two major concepts on the orientation of migrating anadromous fishes have gained wide support: and, while not mutually exclusive, they are, as the frequent clashes in the literature suggest, not entirely compatible.

One of these theories regards the upstream migration of the fish as a purposeful "homing" to the part of the river system in which it was hatched or in which it spent the early stages of

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its life. Memory impressions of the goal or home are implied and the fish is said to be seeking its spawning area. The fish is thought to return to its native stream because that was the place where it was spawned rather than because the stream was more accessible or made more attractive by immediate environmental conditions. The fact that significant numbers of fish have actually been observed to return to the streams from which they originated is frequently used as evidence for this homing viewpoint.

The other theory is that environmental factors control the direction of migration, and therefore physical and chemical conditions such as temperature, current, amounts of dissolved gases, or odors, are thought to determine the ultimate destination of the fish. These factors fluctuate and are duplicated in nature so that migratory fish could go to any stream with these conditions.

Those who support the idea of environmental control of the direction of migration present evidence that the fish responds to its immediate environment at each point of its migration and they look upon the migration itself as merely the sum of the successive responses. The various species are thought to arrive at their separate destinations because they respond in specifically different ways to the existing patterns of environmental stimuli. The return of many fish to the stream of their origin is to be expected, according to this viewpoint, because the patterns of environmental conditions which direct them persist year after year.

Variations of these views may be found expressed under different interpretations of the "parent stream" or "home stream" theory developed by investigators working on salmon migration. An excellent review of major problems and controversial questions in salmon migration is afforded by the symposium, "The Migration and Conservation of Salmon," published in 1939 by the American Association for the Advancement of Science.

SENSORY BASIS OF ORIENTATION

Whether the migratory fish has purpose and seeks its native stream or whether the fish is entirely directed by immediate environmental factors along its route, its orientation must be achieved by some sensory means.

With fish migration, as with bird migration, there has been much speculation over the possible existence of a special sensory perception that is unknown at present. No physical basis for this has ever been found nor have such sensory abilities ever been demonstrated. There is evidence that fish can see, hear, taste, and smell. It is known that they can respond to tactile and kinesthetic stimuli, react to acceleration and nonrectilinear motion, and maintain equilibrium. It has been demonstrated that they can respond to temperature and to various chemical substances by means other than taste or smell. In the absence of any evidence to the contrary, it is reasonable to suppose that these sensory abilities are the ones by which fish are guided while on their migrations. Therefore, it appears logical to explore fully the relation between these known sensory abilities and prevailing environmental patterns before considering hypothetical sensory abilities.

RELATION OF SENSORY ABILITIES TO ENVIRONMENTAL PATTERNS

As the sensory abilities of fishes have been revealed and delineated many investigations have been made to examine their relation to migration. Chidester (1924)[1] pointed out the number and diversity of these investigations as well as their apparently contradictory evidence.

Attention was turned to natural environmental patterns which might have a directional influence upon fish with the known sensory abilities. The physical and chemical gradients which exist along the migration paths of anadromous fishes were examined for their possible role in orienting migrating fish.

The observations of Ward (1920) in Alaska led him to believe that temperature was an important factor in the choice of a spawning stream by sockeye salmon, *Oncorhynchus nerka*. He observed that on the upstream migration the fish pass from swift to slow water and vice versa, that they go from shallow to deep water and vice versa, and that they move from turbid to clear water and vice versa. However, he found that at the junction of two streams the sockeye salmon consistently chose the colder stream and he concluded that temperature was the chief orienting factor.

[1] For references referred to parenthetically, see Literature Cited, p. 395.

The earlier investigations of Chamberlain (1907) in Alaska also indicated that temperature influenced the selection of streams by sockeye salmon. However, Chamberlain found that the sockeye chose the warmer streams.

Foerster (1929) observed the migration of sockeye salmon near Cultus Lake, British Columbia, and found the sockeye at one time entering the colder stream and at another time selecting a warmer stream. He concluded that temperature probably had very little directing influence on the upstream migration of the sockeye salmon. Foerster also made measurements of the *p*H and of the dissolved oxygen in the streams, but was unable to find any correlation between variations in these factors and the selection of streams by the sockeye salmon.

Roule (1933) expressed the opinion that the direction of shad, *Paralosa nilotica rhodanensis* and *Alosa alosa*, migration was controlled by temperature. He pointed out that the migration begins when the river water, pouring into the sea in estuaries, is at a higher temperature than that of the sea. Roule related that in one section of the Rhone River shad fishermen always set their traps on only one bank of the river, whereas along most of the river they set traps on both banks. Investigation revealed that the water on one side of the river was several degrees warmer than on the other due to the influence of a warm tributary upstream. The shad were always found migrating on the warmer side; and they were also observed to turn off the main stream into certain tributaries which were warmer than the main stream. Roule's observations on the behavior of salmon, *Salmo salar*, during migration convinced him that the salmon were indifferent to temperature.

Roule (1914), observing the selection of particular streams by the Atlantic salmon, *Salmo salar*, in its upstream migration to spawning areas, concluded that the proportion of dissolved O_2 in the water was the dominant factor in directing the migration. He maintained that the salmon always choose the water with a higher concentration of dissolved O_2. Roule (1933) suggested that the metabolic condition of the fish results in increased respiratory activity and it becomes polarized toward the more highly oxygenated water. Roule used the word "branchiotropism" to describe deviations in direction brought about by respiratory influences. He maintained that the "branchiopolarity" of the salmon drives it forward and acts as its guide.

Chevey, Roule, and Verrier (1927) blamed the depletion of salmon runs in certain streams on the lack of dissolved O_2 in the streams owing to mill wastes. Their investigations indicated that salmon would not enter a stream with a low dissolved O_2 content. The observation that the shad, *Alosa alosa*, were not affected by the low O_2 content of the water pointed to a marked species difference.

Russell (1934) did not agree with the findings of Roule and his coworkers. He pointed out that in the mouths of certain salmon rivers, such as the Tees and the Tyne, there is a long stretch of heavily polluted water in which the O_2 content may fall very low. However, salmon enter and ascend these rivers.

Shelford and Powers (1915) using a gradient tank technique, found that herring fry, *Clupea pallasi*, would orient to differences in temperature and dissolved gases. Powers became convinced that gradients of CO_2 tension exert an important influence upon the orientation of migrating fishes. Powers and Hickman (1928) measured the CO_2 tension in lakes, in rivers draining lakes, and in rivers which did not drain lakes in the Fraser and the Columbia River systems. They found that, in general, lakes and rivers draining lakes had a lower CO_2 tension (average 0.57 mm. Hg) than rivers not fed by lakes (average 1.05 mm. Hg). Further analysis of the data also indicated that typical mountain streams had higher CO_2 tensions than streams of the lowland.

Powers (1939) pointed to an observation that the sockeye salmon, given a choice, will always choose the fork of a river which drains a lake. The chinook salmon, *Oncorhynchus tshawytscha*, in the same situation apparently is indifferent and moves up either branch. Powers suggested that the sockeye is responding to differences in CO_2 tension in its selection of a stream draining a lake. The lack of a similar response on the part of the chinook salmon was presumably looked upon as a species difference.

The publications of these investigators who were seeking to correlate the observed movements of migratory fishes to gradients of temperature and of dissolved gases were received with great

interest. There has been, however, a general reluctance on the part of many engaged in fishery research to accept some of the conclusions put forth. Those investigators who were convinced of a highly developed homing ability in anadromous fishes found it difficult to reconcile the idea of migrating fishes responding to environmental gradients with that of homing. Many contradictory observations made by other workers in the field, because of a general tendency to avoid negative reporting, seldom reached the literature. Furthermore, field workers who were aware of the enormous difficulties in making dependable observations of the movements of fish in large rivers and streams, particularly with only intermittent observations made over a wide area, felt that the evidence upon which the conclusions were based was inadequate.

In summarizing previous research in this field it might be said that—

(1) The ability of fishes to detect differences in temperature and in amounts of dissolved gases has been established experimentally.
(2) Laboratory (gradient-tank) experiments have also established that differences in temperature and in amounts of dissolved gases can influence the direction of fish movement.
(3) Differences in water temperature and amounts of dissolved gases have been shown to exist in natural waters at points where they might exert an important influence upon the direction of migrating anadromous fishes.
(4) It has been suggested that these physical and chemical differences do influence the orientation of the migrating fish.
(5) Some field observations of migratory-fish behavior appear to show a relation between the direction of migration and gradients of certain physical and chemical factors. These field observations are relatively few, inconclusive, and contradictory.

Thus, it is known that some fishes can orient with reference to certain physical and chemical differences in water, but whether migrating anadromous fishes actually do orient with reference to such differences is not known. The following experiments were undertaken to explore this question with one type of anadromous fish.

EXPERIMENTAL APPROACH

In studying the influence of gradients of physical and chemical characteristics of water upon the orientation of migrating anadromous fishes a direct experimental approach was used. Experiments were undertaken which attempted to measure the directional responses of migrating fishes of the genus *Pomolobus* to certain differences in water characteristics including temperature, *p*H, and amounts of dissolved gases (O_2, N_2, and CO_2).

The experiments were designed to avoid many complications that have to be considered in laboratory experiments with live fish. The experiments were made in the stream in which the fish were migrating so that the fish would not be handled or subjected to the shock of being removed from their natural environment. Tests were made on thousands of fish, and each fish was tested only once so that considerations involving learning could be ignored.

Inasmuch as the special migratory behavior of anadromous fishes is exhibited for only limited periods of time, perhaps only once or twice during the life of the fish, an essential condition of these experiments was that they were conducted while the fish were actually migrating. The importance of this is realized when one considers how greatly the response of a fish to environmental stimuli may differ at various physiological stages of its life. As fingerlings, the fish are found migrating downstream; as maturing adults, they migrate upstream. In those species which survive spawning, the spent fish again migrate downstream. Frequently, individual fish of the same species may be found in a stream responding in very different ways to identical environmental stimuli.

The differences in physical and chemical factors tested were artificially produced in these experiments but the type and magnitude of the differences were within the range commonly found at stream junctions in nature.

MATERIALS AND METHODS

The experiments were conducted in the Herring River at Bournedale, Mass., in 1949 and 1950 during the spring herring runs. The herring run at Bournedale actually consists of two overlapping runs of closely related species. The earlier run, made up of alewives, *Pomolobus pseudoharengus* (Wilson), begins about the first of April and continues until the end of May. The second and smaller run of glut herring, *Pomolobus aestivalis*

(Mitchill), usually starts about the last week of May and lasts until the middle of June.

There are visible external differences by which these two species can be identified. The glut herring is generally smaller than the alewife, has a smaller eye in relation to the head, and when examined out of water has darker dorsal pigmentation. The individual variations in size within the two groups overlap considerably, and in the water each species has the ability to modify its pigment to blend with the background in the matter of a few seconds. Consequently, it is very difficult to distinguish between the two species with any degree of certainty without first removing the fish from the water. Attempts to separate the two species while the experiments were in progress proved to be impractical. When the studies were completed, a careful comparison of the responses shown by the fish in experiments conducted at the beginning of the early run when only alewives were present with those in experiments made near the end of the later run when only glut herring were present, failed to reveal any differences between the responses of the two species.

These anadromous members of the herring family (Clupeidae) proved to be ideally suited to experimental purposes. They are small and migrate in enormous numbers through easily accessible brooks and streams (fig. 1). The construction of the experimental apparatus and the conditioning of water for experiments with these fishes can be done on a smaller, less expensive scale than would be necessary for fishes such as the shad or the salmon. At Bournedale each year during the herring run, more than half a million of these fishes enter the small Herring River (completely fresh water; average flow less than 20 c. f. s.) from the sea water of the Cape Cod Canal and migrate upstream for approximately a mile to their spawning grounds in Great Herring Pond. The experiments were conducted in the stream a short distance below its entrance into Great Herring Pond.

FIGURE 1.—The herring run at Bournedale, Mass. This pool is immediately below the experimental station.

EXPERIMENTAL METHOD

As the fish migrated upstream, they were directed by wire screens into a shallow experimental trough. The upstream end of the trough was divided into two channels of equal size (fig. 2). As a fish progressed upstream through the experimental trough, it was presented with a choice between the two channels. Differences in water

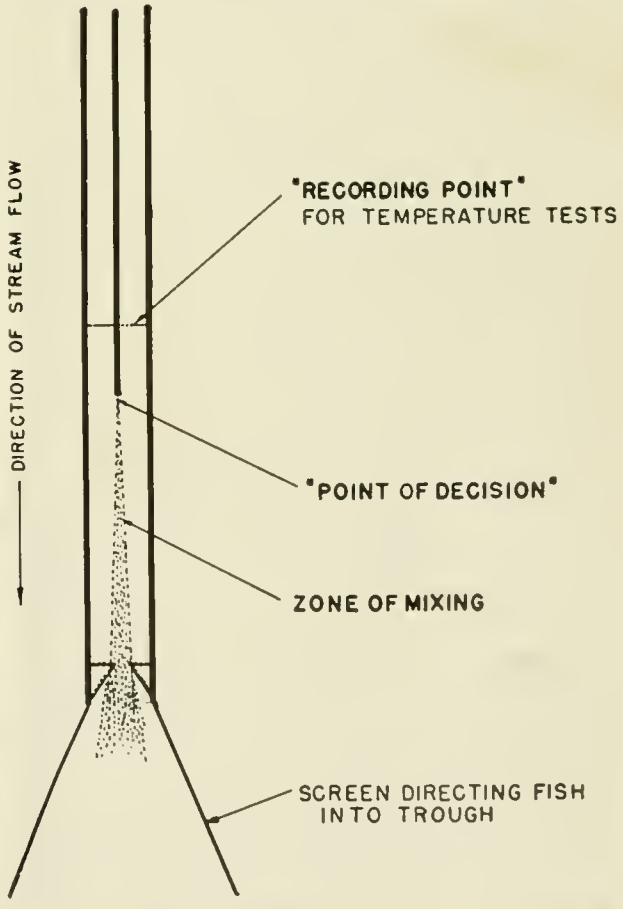

FIGURE 2.—Diagram of experimental trough. Dimensions: 18 ft. long, 21 in. wide, and 10 in. deep.

temperature, in pH, and in dissolved gases between the two channels were created experimentally. The influence of these differences in the physical and chemical characteristics of water upon the orientation of the migrating fish was measured by the number of fish choosing each channel.

The experimental trough was 21 inches wide, 10 inches deep, and 18 feet long. It was open at both ends so that when it was alined with the direction of stream flow and partially submerged, the water flowed freely through it. The two channels in the upstream end of the trough were 10 feet long and 10 inches wide. A 10-inch channel width was chosen because it was approximately equal to the length of the fish and would allow enough room for normal swimming movements and turning. The experimental trough could be raised or lowered in the water in order to create any desired depth of flow regardless of the natural fluctuation in the water level of the stream. The flow of water through the trough was maintained at a depth of 6 to 8 inches, while the velocity of water through the trough varied, depending on stream conditions, from a minimum of 1 foot a second to a maximum of 2 feet a second.

The trough was stained a dull mahogany to provide a dark background for the fish so that their behavior would be as natural as possible. Exploratory tests the previous year had shown that a light background made the fish extremely nervous and excitable when they were in the shallow water and confinement of the experimental trough. The trough was also placed in the stream several weeks before tests were begun to reduce the possibility of odors, or other factors that might be unfamiliar or objectionable to the fish.

To prevent light inequalities between the two channels resulting from shadows, the experimental trough was shaded from direct sunlight by a canvas canopy (fig. 3).

At the downstream end of the trough a wire-screen gate was installed to control the entrance of the fish into the experimental trough. The necessity for such a device became apparent during preliminary exploratory tests in which the entrance of the fish was unrestricted. When several fish entered at the same time, they frequently exhibited a schooling tendency and all followed the choice of the leader. Their behavior was such that it seemed probable that only one decision was

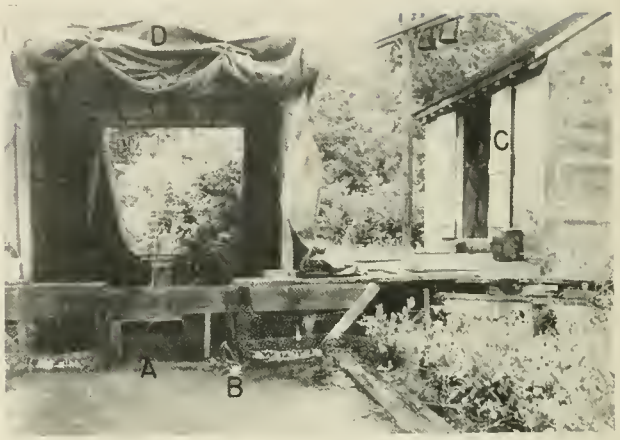

FIGURE 3.—General view of experimental station, Herring River, Bournedale, Mass., 1950.

A. Entrance for upstream migrants.
B. Bypass exit for downstream migrants.
C. Laboratory for chemical determinations.
D. Light-control arrangement.

actually made for the entire school. There were instances of schools splitting, with all those on the left side entering the left channel, and all those on the right side entering the right channel, suggesting that perhaps in these cases spatial relations alone were involved. There were many variations in such group behavior and they were difficult to interpret in a quantitative way. To avoid the problem completely, an entrance gate was designed. Through this gate (figs. 4 and 5) the fish were allowed to enter, one at a time, and only after the previous one had made its decision and was completely out of the trough.

The entrance gate also served to center the fish so that as it entered the experimental trough it was subjected to a mixture of the waters of both channels. Thus, the fish started in the center of a strong transverse gradient (fig. 2) and almost any lateral movement resulted in its being subjected to water of a different quality.

PROCEDURE

As the fish progressed upstream in the trough to the point where it had to choose between the two channels (the "point of decision" in fig. 2), it usually moved from one side of the trough to the other, alternately approaching each channel until it finally entered one. In those tests in which both channels were completely unobstructed the choice was recorded when the fish had completed

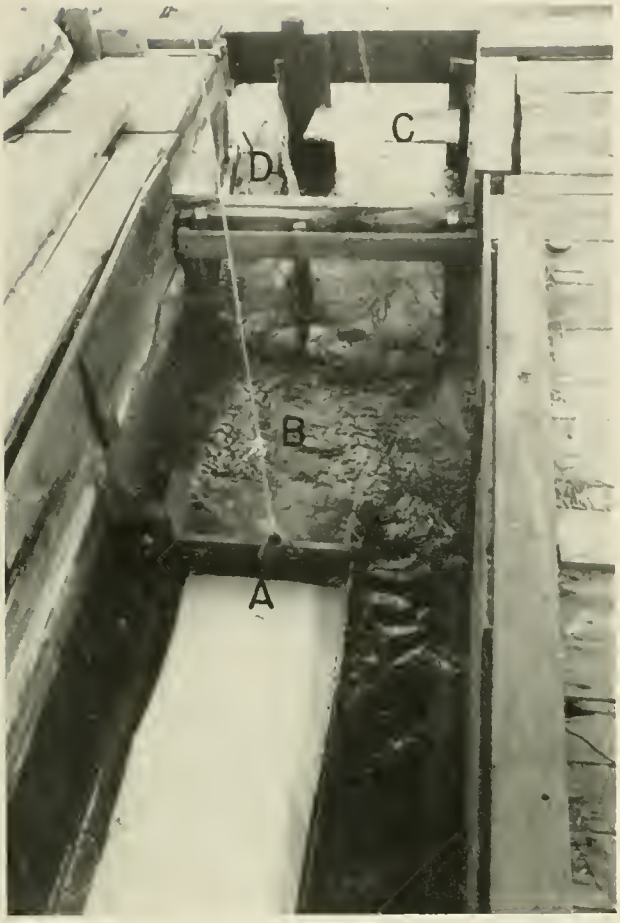

FIGURE 4.—Entrance to experimental trough.

A. Entrance gate (closed).
B. Retaining pool.
C. Retaining-pool gate (open).
D. Bypass for downstream migrants.

(The white cloth on the bottom of the trough was for photographic purposes and was not present during the tests.)

its passage through the channel and was entirely clear of the trough. This system of recording decisions permitted the fish to change its choice of channels at any stage of its progress by turning back and entering the other channel.

During the experiments in which the water was being modified by heating, the reluctance of the fish to pass through the heating apparatus in the upstream ends of the channels, resulted in considerable delay. To save time a "recording point" (fig. 2) was chosen below the heating apparatus. When this arbitrary point which was 20 inches (approximately twice the length of the fish) from the entrance to the channel was

FIGURE 5.—Entrance gate. The fish were allowed to enter, one at a time, through a screen gate (shown open).

(The white cloth was not present during the tests.)

reached, the fish was considered to have made its decision and the result was recorded. When once the fish had passed the recording point if its forward progress was too slow, it was urged to continue on out of the trough by taps on the trough with a stick immediately behind the fish. When the fish was completely out of the trough, the entrance gate was raised again to allow another to enter.

Before each series of tests, any necessary adjustments of experimental conditions were made and water samples and temperature measurements were taken. The fish were then allowed to enter the trough one at a time. It usually was found convenient to run approximately 25 to 30 individual tests in succession before the measurements were taken again. The average time for such a series of tests was about 40 minutes, although it fluctuated considerably depending upon the behavior of the fish.

CONTROLS

Every effort was made to keep conditions, e.g., light, depth of water, rate of flow, turbulence, as uniform as possible in both channels so that any directional response would be due solely to the factor being tested. Whenever major adjustments in the experimental conditions had been made, before tests with modified water were begun, a series of control tests was run to ensure

that such uniform conditions prevailed. The results of these tests are summarized in table 1.

TABLE 1.—*Daily totals of control tests made to ensure that uniform conditions existed in both channels of the experimental trough, 1949*

Date	Number of fish entering—	
	Left channel	Right channel
April 30	91	89
May 1	49	39
2	54	48
3	68	73
7	97	91
8	58	49
11	19	15
12	20	22
14	71	54
15	81	83
16	49	47
19	25	29
22	59	49
23	47	58
24	24	24
30	29	30
Total	841	800
Percent	51.3	48.7

To minimize the possibility of some unrecognized factor influencing the choice of the fish, control and test channels were alternated between each series of tests. Such alternation resulted in any "nonalternating" influence being cancelled out when the figures were totaled. An example of the pattern of controls and tests is given in table 2.

TABLE 2.—*Example of the pattern of controls and tests, May 15, 1949*

[Tests listed in chronological order]

Left channel		Right channel	
Water characteristic [1]	Number of fish	Water characteristic [1]	Number of fish
Control	18	Control	17
CO_2	11	Control	31
Control	26	CO_2	19
Control	25	Control	27
Control	35	CO_2	12
CO_2	11	Control	34
Control	16	Control	16
Control	33	CO_2	17
CO_2	9	Control	26
Control	22	Control	23
CO_2	8	Control	31
Control	31	CO_2	14

[1] Control, water unmodified; CO_2, gaseous CO_2 added.

During tests involving temperature differences of greater than 1 degree centigrade, it was necessary to have a greater number of heaters in one channel than in the other. To be certain that the response shown was the result of temperature differences rather than differences in hydraulic conditions created by the unequal distribution of heating apparatus, a series of control tests was run with the heaters in place but with the power turned off. The results of the control tests which were interspersed with the actual temperature tests are shown in table 3. They indicate that the presence of the nonoperating heaters had little or no effect upon the choice of channels made by the fish.

TABLE 3.—*Control tests during temperature experiments, 1950*

[Immersion heaters in place but power turned off]

Date and time	Number of fish entering—		Number of immersion water heaters in—	
	Left channel	Right channel	Left channel	Right channel
May 13, 3:45 p. m	16	17	5	5
14, 6:25 p. m	27	25	0	10
15, 8:00 a. m	9	8	0	11
20, 10:00 a. m	12	12	0	11
24, 2:30 p. m	13	14	0	11
24, 3:30 p. m	14	13	0	11
25, 4:00 p. m	26	27	0	11
26, 9:15 a. m	15	12	0	11
26, 11:30 a. m	12	15	0	11
27, 10:30 a. m	21	30	0	8
27, 11:55 a. m	9	10	0	8
27, 1:30 p. m	11	15	0	8
27, 4:00 p. m	8	7	0	8
27, 5:00 p. m	27	34	0	8
28, 12:40 p. m	13	12	0	8
28, 2:00 p. m	13	11	0	8
28, 5:30 p. m	13	12	3	8
June 3, 8:15 a. m	7	5	0	11
6, 10:30 a. m	4	4	0	11
7, 11:15 a. m	13	15	0	11
Total	283	298		
Percentage	49	51		

WATER MODIFICATION

Temperature

The modification of the water temperature was accomplished by the use of industrial electrical immersion water heaters. These heaters (32 a., 7.5 kw., 230 v.) were of the tubular type and shaped in a simple loop so as to fit easily into the channels of the experimental trough (fig. 6). Each of the 11 heaters was connected separately to the main circuit and could be turned on or off at will without interfering with the operation of any of the other heaters. The arrangement was simple and flexible and made a graded control of temperature possible.

Gaseous Content

The gaseous content of the water was modified by the introduction of specific gases. These gases (O_2, N_2, and CO_2) were bubbled into the water at the upstream end of the trough directly in front

FIGURE 6.—Upstream end of experimental trough during temperature tests. All immersion water heaters are in place for maximum temperature difference.

(Shade on left was raised to allow light for photographic purposes. During the experiments no shadows were present.)

FIGURE 7. Device for modifying gaseous content of water. The device contained two separate batteries of aerators so that the two channels could be modified independently at the same time.

of the channel or channels in which the water was to be modified.

The device used to accomplish this (fig. 7) consisted of two batteries of porous-stone aerators of the type commonly used in small aquariums. Each battery of aerators produced a band of very fine bubbles. The incorporation of two separate batteries in the same device made it possible to modify independently the water of both channels at the same time.

Nongaseous Chemicals

The nongaseous chemicals used to modify water in experiments were first dissolved in a carboy of water from the stream. They were then introduced at a controlled rate into the upstream end of one of the channels through a colorless plastic tube positioned horizontally an inch above the floor of the trough at right angles to the direction of stream flow. Small holes were bored in the plastic tube at short intervals to allow an even distribution of the carboy liquid throughout the channel.

MEASUREMENTS

Water Samples

Water samples were collected in wide-mouthed 100-milliliter bottles at the downstream end of each channel. Sample bottles were stoppered while still under water to avoid any gaseous exchange with the air. The samples were collected simultaneously in both channels and were immediately brought into the field laboratory where the chemical determinations were begun at once.

Titrations

Titrations were done with a Beckman *p*H meter. The water-sample bottles were calibrated with the solid stoppers on so that the exact amount of water in each sample was known without further measurement. The titrations were performed in the sample bottles to avoid any opportunity for the modification of the gaseous content of the water due to exposure to air in pouring.

Hydrogen-ion Concentration

Measurements of hydrogen-ion concentrations were made to within 0.03 *p*H unit with a Beckman *p*H meter. A Hellige pocket color comparator was used for rapid *p*H measurements (to within 0.1 *p*H unit) during adjustment of valves while setting up experimental conditions and during a number of the earlier exploratory experiments.

Alkalinity and HCO_3.

In the range of *p*H in which the experiments were made (*p*H 7 to *p*H 6) the alkalinity was assumed to equal the concentration of HCO_3. Methyl-orange alkalinity was measured (American Public Health Association 1946) by titrating the sample with H_2SO_4 to an end point of *p*H 4.4.

Carbon Dioxide

The free, or uncombined, CO_2 content of the water was measured in two ways. Some of the measurements were made directly by titration of the sample with NaOH (American Public Health Association 1946) to an end point of *p*H 8.2. Other determinations of free CO_2 were made indirectly by measuring alkalinity (methyl orange) and *p*H and then determining CO_2 by the graphic method of Moore (1939). The measurements were made to within 0.1 p. p. m. CO_2. Those measurements made directly by titrating with NaOH were slightly lower than the measurements made indirectly by the graphic method. Therefore, in comparing the water of the two channels only one method was used for each pair of measurements. The range of conditions under which the measurements were made is indicated by figure 8 which shows CO_2 measurements made during the experiments.

During the series of tests which examined the orientative influence of CO_2, water was modified by the introduction of gaseous CO_2. Addition of gaseous CO_2 to the almost unbuffered water of the stream produced several effects. It increased the concentration of free CO_2 and it decreased the *p*H. It also raised the partial pressure, or tension, of CO_2 in the water. Examples of data from individual tests (table 4) illustrate the first two of these effects. It will be noted that the concentration of HCO_3 was largely unaffected. In the range of *p*H in which the experiments were made (*p*H 7 to *p*H 6), carbonates were not present.

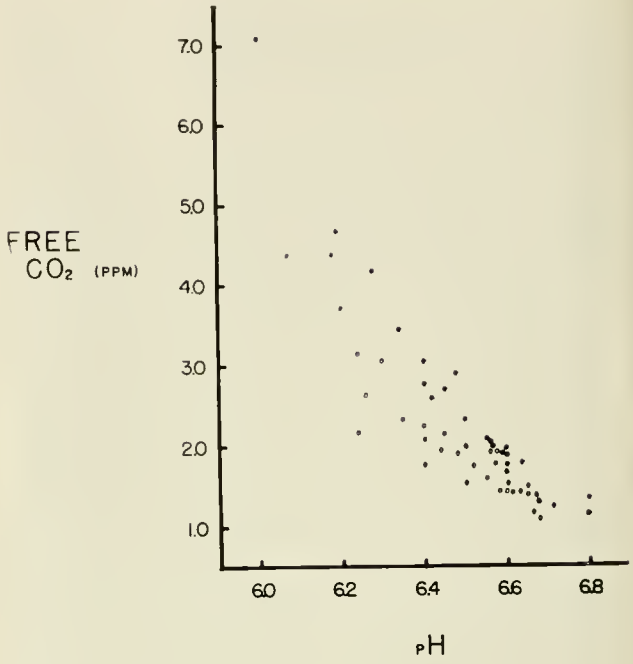

FIGURE 8.—Free CO_2 measurements, May 1950. Only measurements of samples of unmodified stream water and water modified by the addition of gaseous CO_2 are included. The samples were taken under a wide variety of stream and weather conditions.

Water was modified by addition of $K_2H(PO_4)$ during the tests of the orientative influence of *p*H. Examples of data from individual tests are given in table 4. In these tests the changes in *p*H were of approximately the same magnitude as the changes in *p*H in the tests in which CO_2 was added (although $K_2H(PO_4)$ raised the *p*H while CO_2 lowered it). The addition of $K_2H(PO_4)$, however, had much less effect upon the concentration of free CO_2.

During this investigation, measurements of CO_2 were restricted to the convenient and widely accepted methods available for measuring the amount of free CO_2. The importance of measuring dissolved gases in terms of partial pressures

TABLE 4.—*Examples of chemical measurements made during individual tests, June 11, 1950*

[Stream temperatures, 19° to 19.4° C.]

Channel	Water characteristic [1]	Hydrogen-ion concentration	Alkalinity or HCO_3	Carbon dioxide
			P. p. m. $CaCO_3$	*P. p. m.*
Left	CO_2	6.40	4.04	3.05
Right	Control	6.57	3.98	2.06
Difference		.17	.06	.99
Left	Control	6.57	3.88	1.95
Right	CO_2	6.18	3.76	4.68
Difference		.39	.12	2.73
Left	Control	6.52		[2] 1.70
Right	$K_2H(PO_4)$	6.97		[2] 1.62
Difference		.45		.08
Left	$K_2H(PO_4)$	6.94		[2] 1.71
Right	Control	6.57		[2] 1.78
Difference		.37		.07

[1] CO_2, gaseous CO_2 added; control, water unmodified; $K_2H(PO_4)$, $K_2H(PO_4)$ added.
[2] Samples titrated with NaOH.

when considering their physiological effects upon organisms is recognized. The ability of a gas to diffuse through a membrane depends upon the tension of the gas in solution. Therefore, the tension of the gas is critical where, as in respiration, an actual gaseous exchange is made. However, very little is known of the sensory mechanism by which fish detect differences of CO_2; nor is it known whether CO_2 must actually permeate a membrane to affect the sensory organs. Under the circumstances of these experiments, where both channels receive water from the same source under identical conditions, the CO_2 tension would be directly proportional to the amount of free CO_2 present. Therefore, the relative amounts of CO_2 in the two channels may be used as indexes of the relative CO_2 tensions.

Oxygen

The amount of dissolved oxygen was determined by the standard Winkler method (American Public Health Association 1946) after preliminary orientation tests (Ellis, Westfall, and Ellis 1948) for the presence of interfering substances proved to be negative.

Temperature

Temperatures were measured to 0.1° C. by the use of a mercury thermometer held horizontally in the water with its long axis in the direction of the current. The measurements were taken at the downstream end in each channel with the center of the thermometer at a point 2 inches from the bottom of the trough (the level at which the fish usually swam) and 2 inches from the wall which divided the trough into two channels.

Velocity

The velocity of the water flowing through the trough was measured by means of an impeller-type current meter. Measurements were accurate to within 0.2 feet per second, and represent the average velocity of the water over a 90-second period of time. The measurements were taken at the downstream end of each channel at a point halfway between the channel walls.

ABERRATIONS IN EXPERIMENTAL CONTROL

Throughout the experiments, measurements of physical and chemical water characteristics such as temperature, velocity, *p*H, and amounts of dissolved gases were much more precise than the experimental control of these characteristics. Hydraulic conditions above the head of the experimental trough created a periodic eddying (every 5 to 15 seconds) which resulted in a fluctuation in the rate of flow alternately in each channel. During tests in which water characteristics were being modified, eddying caused a periodic fluctuation in the degree of modification. For example, during tests in which the water was modified by heating, eddying resulted in a temperature fluctuation of approximately 0.5° C. in the channel being modified.

Temperature measurements to within 0.1° C. were made almost instantaneously, and the extent of the temperature fluctuation was easily measured by a comparison of maximum and minimum temperature readings. However, measurements of other water characteristics such as velocity, *p*H, and amounts of dissolved gases were average measurements. Velocity measurements (read in terms of propeller revolutions per unit time) represented an average velocity for a 90-second period of time. The manner in which the water samples were taken for measurements of *p*H and amounts of dissolved gases tended to collect a mixture of the water flowing through a channel over a period of time greater than the time for a complete cycle of eddy fluctuation and so these measurements also represent measurements of average conditions.

Such average measurements gave no clear indication of the degree of fluctuation.

Some of the other experimental conditions also could not be controlled completely. The depth of the water in the trough, maintained at 6 to 8 inches at the downstream end of the two channels, varied from 4 inches to 10 inches at the ends of the trough when the trough deviated from a horizontal position. The downstream end of the trough had a tendency to settle as a result of the clogging of the screen entrance gate by floating organic debris. Variations of this sort affected the channels equally, however, and probably are of little significance.

During the experiments in which water was heated electrically there frequently was a vertical variation in the temperature of the water in the modified channel due to inadequate mixing of the heated water. This was particularly true when only a few heaters were in operation. At such times, the variation was as much as 0.4° C. from the warmer water near the bottom of the channel to the cooler water near the surface. The temperature measurements, made 2 inches from the bottom of the channel (the level at which the fish usually swam), were always of the maximum temperature.

In interpreting the data collected during these experiments, such variations in experimental conditions must be taken into consideration, particularly when thresholds are concerned. The thresholds for the responses of the fish may actually be lower than those indicated by the data.

EXPERIMENTS

ORIENTATIVE INFLUENCE OF TEMPERATURE

Experiments were conducted in which the migrating fish were presented with a choice between waters of two different temperatures. The responses of the fish (table 5) indicated a preference for the warmer water.

The stream temperature during these experiments ranged from 11.1° to 22.3° C. The temperature differences between channels, created by heating the water of one channel, were varied from 0.4° to 3.0° C. The threshold of the response appeared to be at a temperature difference of approximately 0.5° C.

Periodic eddying which caused a fluctuation in the water temperature of the channel being modified (see Aberrations in Experimental Control, p. 385) was probably responsible for the apparently intermediate nature of the response to temperature differences of 0.5° to 1.0° C. The temperature difference values given in tables 5 and 6 are maximum values. The minimum values were approximately 0.5° C. less. For example, during tests at the recorded temperature difference of 0.7° C., for at least part of the time, the temperature difference was approximately 0.2° C.

Therefore, only at recorded temperature differences above 1.0° C. was the threshold difference of 0.5° C. exceeded continually throughout the entire test.

TABLE 5.—*Response to temperature differences as shown in experiments of May 7 to June 8, 1950*

[Stream temperatures, 11.1° to 22.3° C.]

Water temperature difference between channels [1] (Centigrade)	Number of decisions	Entered channel with—	
		Warmer water	Cooler water
		Percent	*Percent*
0.4°	98	[2] 49	51
0.5°	109	57	43
0.6°	51	61	39
0.7°	180	63	37
0.8°	427	60	40
0.9°	471	61	39
1.0°	76	63	37
Total	1,314	[3] [4] 61	39
1.1°	22	77	23
1.2°	98	80	20
1.3°	136	76	24
1.4°	100	76	24
1.5°	142	77	23
1.7°	98	79	21
1.8°	107	80	20
1.9°	27	78	22
2.0°	83	80	20
Total	813	[3] 78	22
2.2°	213	73	27
2.3°	132	73	27
2.4°	108	83	17
2.5°	28	75	25
2.7°	24	79	21
3.0°	12	75	25
Total	517	[3] 76	24

[1] Temperature differences are maximum values. Minimum temperature differences were approximately 0.5° C. less.
[2] No response.
[3] Response.
[4] See notes on eddying phenomenon, p. 385.

Taking the eddying into account, the intermediate nature of the response to temperature differences from 0.5° to 1.0° C. should probably be discounted and considered as due to imperfect experimental conditions. The data would then be interpreted as describing a uniform ungraded response to temperature differences greater than the threshold.

RELATION OF TEMPERATURE RESPONSE TO TEMPERATURE LEVEL

Tabulation of experimental data according to stream temperature levels (table 6) revealed a general tendency for the response to temperature differences between 0.5° and 1.0° C. to decrease as the temperature level of the stream increased. When the temperature differences between channels were greater than 1.0° C., the temperature level of the stream had no discernible influence upon the response of the fish.

TABLE 6.—*Relation of temperature response to temperature level*

[Retabulation of data from table 5. Stream temperature levels include +0.9° C. (e. g., 11° C. includes temperature levels to 11.9° C.)]

Stream temperature level	Number of decisions	Entered channel with—	
		Warmer water	Cooler water
		Percent	*Percent*
Group A:[1]			
11° C.	139	65	35
12° C.	178	65	35
13° C.	185	65	35
14° C.	274	60	40
15° C.	116	59	41
16° C.	124	55	45
17° C.	66	55	45
18° C.	85	54	46
19° C.	147	53	47
Group B:[2]			
11° C.	35	80	20
12° C.	43	79	21
14° C.	238	77	23
15° C.	217	80	20
16° C.	159	75	25
17° C.	290	76	24
18° C.	198	77	23
20° C.	123	82	18
22° C.	27	78	22

[1] Temperature difference between channels, 0.5° to 1.0° C.
[2] Temperature difference between channels, 1.1° to 3.0° C.

Taking into account once again the eddying condition (see p. 385), the data indicate that the responses of the fish were affected by the temperature level only when temperature differences of threshold magnitudes were concerned. The evidence suggests a possible relation between this phenomenon and the type of threshold phenomena described by Weber's law. Weber (1846) believed the threshold of difference to be proportional to the intensity of stimulus. Although the ratio of these two factors has since been shown to be variable, a tendency for the threshold of difference to increase with an increase in intensity of stimulus has been observed. The experiments at Bournedale, planned with other purposes in mind, did not produce the type of data necessary to examine this particular aspect of the response to temperature differences. However, it seems very probable that the decrease in the response of the fish (shown in group A, table 6) was due to an increase in the threshold of the response to temperature differences as the temperature level of the stream increased.

ORIENTATIVE INFLUENCE OF CO_2

The migrating fish were presented with a choice of waters having different amounts of free, or uncombined, CO_2. The difference in free CO_2 between the waters of the two channels was established by the direct addition of gaseous CO_2 to the water of one channel while the other remained unmodified. During some of the tests this procedure was varied by the addition of the gaseous CO_2 to both channels but at different rates. Throughout the tests the fish indicated a definite preference for the water with the lower free CO_2 content (table 7).

TABLE 7.—*Responses to differences in CO_2 as shown in experiments, May 1–30, 1949, and May 7–June 9, 1950*

Free CO_2 difference between channels	Number of decisions	Entered channel with—	
		Lower CO_2	Higher CO_2
		Percent	*Percent*
>4.0 p. p. m.	1,120	73	27
1.4 p. p. m.	128	77	23
0.6 p. p. m.	663	71	29
0.3 p. p. m.	216	69	31
0.2 p. p. m.	157	59	41

NOTE.—Unmodified stream water varied from 0.7 p. p. m. free CO_2 to 2.9 p. p. m. free CO_2 and pH 6.9 to pH 6.4. Stream temperatures 11.1° to 22.3° C. CO_2 differences listed include differences ±0.1 p. p. m. of listed differences except 0.3 which includes only +0.1 p. p. m.

Whether the fish in the CO_2 experiments were responding to differences in free CO_2 or to associated differences in HCO_3 is not actually known. The data (table 7) indicate that if the response was to differences in the amount of free CO_2, the threshold of the response lies below differences of 0.3 p. p. m. If the response of the fish was to differences in HCO_3, then the threshold of the response must be much lower. During most of the tests in which the differences in free CO_2 were less than 1.0 p. p. m., the differences in HCO_3 were not even measurable by the method of measurement used (i. e., they were less than 0.1 p. p. m. HCO_3 as $CaCO_3$). It seems more probable that the response of the fish was a response to free CO_2.

The experiments do not indicate whether the response of the fish (assuming that the response was to free CO_2) was to differences in the amount

of free CO_2 or to differences in CO_2 tension. The difference in CO_2 tension associated with a difference of 0.3 p. p. m. free CO_2 under the conditions of these experiments would be approximately 0.1 mm. Hg.

The response of the fish to differences in CO_2 (whether it was to the amount of free CO_2, to the CO_2 tension, or to associated HCO_3) was similar to the response of the fish to temperature differences in that it appeared to be a uniform response to all differences above the threshold difference.

RELATIVE ORIENTATIVE INFLUENCE OF CO_2 AND TEMPERATURE

As the evidence was acquired indicating that differences in temperature and differences in CO_2 could influence the orientation of the migrating fish, the need for some information on the relative influence of the two factors became increasingly obvious. Under the controlled conditions of the experiments, where all factors other than the one used for testing were maintained equal in both channels, the fish might show as great a response to a relatively minor influence as they would to an important or dominant factor. To examine the relative orientative influence of CO_2 and temperature, two groups of experiments were undertaken. In one set of experiments the directional influences of the two factors were arranged so as to be in conflict. The differences in CO_2 favored the choice of one channel, while the differences in temperature favored the selection of the other. In a second group of experiments the differences both in CO_2 and in temperature favored the selection of the same channel.

The data (table 8) collected indicate that the relative importance of the two orienting factors depends upon their quantitative relationships. By altering the relative amounts of heat and of CO_2 added to the water, it was possible to demonstrate circumstances under which either factor could balance or even dominate the other when the factors were in opposition. The data also suggest that when the two factors are not in opposition they may actually augment each other and together provoke a response in a greater number of fish than either factor could produce alone.

ORIENTATIVE INFLUENCE OF pH

In the preceding experiments involving the addition of gaseous CO_2 to the water, the differences in the amount of free CO_2 between the two channels were always accompanied by differences in *p*H (see table 4). The question arises as to whether the response shown by the migrating fish is to the differences in CO_2 or to the accompanying differences in *p*H.

An attempt was made to answer this question experimentally with the migrating fish. It was necessary to use a substance which would, when added to the water, modify the *p*H of the water to the same degree that it was modified during the CO_2 experiments (see table 9) without, at the same time, materially affecting the amount of free CO_2 in the water. It was also necessary that the substance be one to which the fish would not respond by means such as taste or smell. To avoid the difficulties of determining whether the response of a fish was to the taste or to the smell of a chemical, or whether its response was to *p*H differences created by that chemical, it was necessary to select a substance to which the fish did not respond at all.

In one of a series of exploratory tests (table 10) NaOH was used to modify the water. There was no response to a difference in *p*H of 0.1 (compare with response to *p*H difference 0.1 created by the addition of gaseous CO_2, table 9). However, it will be noted that when the difference in *p*H was greater than 1.0 *p*H unit, the fish favored the

TABLE 8.—*Relative orientative influence of CO_2 and temperature as shown in tests made June 3–11, 1950*

Relation of factors	Water temperature difference between channels	Free CO_2 difference between channels	Number of decisions	Entered channel with—			
				Warmer water and higher CO_2	Cooler water and lower CO_2	Warmer water and lower CO_2	Cooler water and higher CO_2
	° C.	P. p. m.		Percent	Percent	Percent	Percent
Opposing	0.5 to 0.6	>7.0	99	24	76		
	1.8 to 2.1	0.5 to 2.0	129	62	38		
	1.8 to 2.4	2.4 to 7.0	169	48	52		
Augmenting	2.0 to 2.4	0.5 to 2.0	154			83	17

NOTE.—Stream temperatures, 16.9° to 22.2° C. Unmodified stream water, 0.7 p. p. m. to 2.1 p. p. m. free CO_2; pH 7.0 to pH 6.5.

TABLE 9.—*Experiments with CO_2 tabulated according to differences in pH, May 1949*

pH difference between channels [1]	Number of decisions	Percent entering—	
		Higher CO_2	Lower CO_2
>1.00	650	30	70
0.10	663	29	71
0.05	114	28	72
<0.05	157	41	59

[1] Range, pH 6.0 to pH 6.8.

TABLE 10.—*Experiments with NaOH tabulated according to differences in pH, May 24, 1949*

pH differences between channels	Number of decisions	Percent entering—	
		Control channel [1]	Channel with NaOH added [2]
>1.00	267	39	61
0.10	104	48	52

[1] Unmodified stream water, pH 6.6 to pH 6.8; low pH; high CO_2 content.
[2] High pH; low CO_2 content.

modified water. Although CO_2 was not measured in this test it seems very probable that the difference in free CO_2 which would be associated with the large difference in *p*H would exceed the threshold 0.3 p. p. m.

After several acids and bases were tried, an experiment was undertaken using $K_2H(PO_4)$ as the modifying agent. The data collected (table 11) reveal no indication of a response on the part of the fish although differences in *p*H were present. These differences in *p*H were of the same magnitude as those in many CO_2 tests in which the fish responded. The accompanying table 12 of free CO_2 measurements made while the tests were in progress shows that during the tests differences of free CO_2 between channels were very small, generally less than the precision of measurement.

TABLE 11.—*Orientative influence of pH as shown in tests made June 10–12, 1950*

[Differences in pH include differences ±0.1 pH unit]

$K_2H(PO_4)$ added	Unmodified control	Difference in pH	Number of decisions	Entered channel with—	
				High pH	Low pH
pH	*pH*			*Percent*	*Percent*
6.7	6.5	0.2	148	49	51
6.9	6.5	.4	127	51	49
7.1	6.5	.6	141	47	53
7.3	6.5	.8	20	50	50
Total			436	49	51

TABLE 12.—*Measurements of free CO_2 taken during the tests shown in table 11*

[Samples titrated with NaOH]

$K_2H(PO_4)$ added	Unmodified control	Difference in free CO_2	Difference in pH
P. p. m.	*P. p. m.*	*P. p. m.*	
1.94	1.96	0.02	0.2
1.62	1.69	.07	3
1.71	1.78	.07	4
1.62	1.70	.08	4
1.31	1.45	.14	6

On the basis of the evidence from this experiment, it would seem reasonable to conclude that the response shown by the migrating fish in the previous tests was a response to differences in CO_2 rather than a response to differences in *p*H.

EXPERIMENTS USING NITROGEN AND OXYGEN

Nitrogen

During the tests with CO_2, particularly those tests in which the CO_2 had been added to only one of the two channels, the possibility had to be considered that the physical presence of many bubbles in the modified channel might be influencing the choice of the fish. To eliminate this possibility nitrogen was used as a control. The gaseous nitrogen was bubbled into the water of one of the channels in the same manner and at the same rate as the CO_2 in the previous experiments. The addition of the N_2 produced no measurable difference in the amount of dissolved O_2. The data (table 13) reveal that the fish failed to show any response to the nitrogen or to the presence of the many bubbles produced. The nitrogen was then used as a control in a series of CO_2 tests. The results of these tests show the same response to CO_2 that was shown in previous tests, again indicating that the presence or absence of the bubbles had no influence upon the choice of the fish.

Oxygen

To investigate the orientative influence of O_2, the migrating fish were presented with a choice of waters which contained different amounts of dissolved O_2. The water of one of the channels was modified by the addition of gaseous O_2. The experiment, however, was severely limited by the fact that the water of the stream was already more than 100 percent saturated. The data in table 13 show that the fish did not respond to a relatively small difference in O_2 under these conditions. The

TABLE 13.—*Experiments testing orientative influence of oxygen and nitrogen*

Factor	Number of decisions	Entered control channel	Entered channel with—		
			N_2 added	CO_2 added	O_2 added
		Percent	*Percent*	*Percent*	*Percent*
Nitrogen bubbles	300	50	50		
Nitrogen (control)	477		71	29	
Oxygen [1]	344		50		50

[1] Stream temperature, 15.4° to 19.1° C. O_2 content of unmodified stream water, 10.5 to 10.7 p. p. m. O_2 difference between channels, 1.1 p. p. m.

experiments unfortunately provide no information on the possible effect of differences in O_2 at lower values where differences may be very important.

OTHER FACTORS INFLUENCING ORIENTATION

Although the major experimental efforts of this investigation were concerned with the orientative influence of temperature and dissolved gases, exploratory experiments also examined the influence of other factors.

The influence of water velocity upon the orientation of the migrating fish was explored by subjecting the fish to a choice between waters of different velocities. The difference in velocity between the two channels was created by placing a glass plate across the upstream entrance to one of the channels, restricting the amount of water entering that channel and so reducing the velocity of the water in the downstream end of the channel. The response of the fish (table 14) indicated that water velocity could be a factor in fish orientation.

The influence of water turbulence upon the orientation of the fish was explored in a similar manner. The turbulence in one of the channels was reduced by placing glass plates, several feet in length, in the center of the channel parallel to the channel walls. This produced a flow which was smooth and laminar in appearance. In the other channel, small glass plates were set at an angle to create eddies which produced a visible turbulence. Most of the fish selected the channel with less turbulence (table 15). CO_2 was then added to the channel with less turbulence in order to discover the relative influence of turbulence and CO_2. The data indicate that CO_2 had the greater orientative influence.

TABLE 14.—*Orientative influence of velocity*

Water velocity		Number of decisions	Entered channel with—	
Right channel	Left channel		Higher velocity	Lower velocity
Ft./sec.	*Ft./sec.*		*Percent*	*Percent*
1.5	0.7	26	85	15
0.7	1.0	26	65	35

TABLE 15.—*Orientative influence of turbulence and CO_2*

Influence of—	Number of decisions	Entered channel with—	
		Maximum turbulence	Minimum turbulence
		Percent	*Percent*
Turbulence	26	32	68
Turbulence and CO_2	27	70	[1] 30

[1] CO_2 added, 4 p. p. m.

An exploratory experiment was made which indicated that visual factors may influence fish orientation. The downstream end of one channel was partially blocked (see fig. 9). The fish normally swam within a few inches of the bottom of the trough so that the "obstacle" did not interfere in any physical way with their progress. However, most of the fish entered the channel which was completely unobstructed. To examine the relative influence of this visual factor and temperature, the water of the partially blocked channel was heated 2° C. The data (table 16) show that under these conditions temperature was the dominant orienting factor.

These tests were crude experiments of an exploratory nature. There undoubtedly were some velocity differences involved in the turbulence tests. The partial block at the downstream end of one of the channels in the tests involving the visual factor probably created slight differences

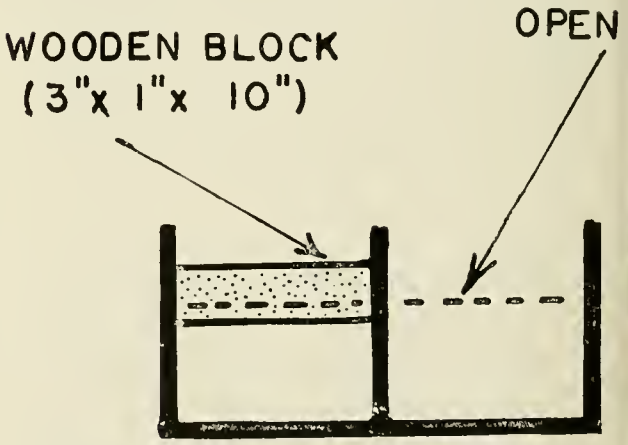

FIGURE 9.—"Visual" factor (exploratory tests).

TABLE 16.—*Orientative influence of the visual factor*

Influence of—	Number of decisions	Entered channel that was—	
		Open	Obstructed
		Percent	*Percent*
Visual factor	89	65	35
Temperature and visual factor	93	10	1 90

[1] Heat added, 2° C.

in hydraulic conditions between the two channels. The experiments were done with relatively small numbers of fish and the degree of the response should not be interpreted too literally. However, the experiments are presented here because they do indicate that characteristics of flow, such as velocity and turbulence, can have a directional influence upon migrating fish. They also indicate that, under some circumstances at least, visual factors are capable of influencing fish orientation.

THE 3 : 1 RATIO OF THE RESPONSE

The explanation for the persistence of the approximately 3 : 1 ratio in the response of the fish to temperature differences and to CO_2 differences is not readily apparent. The absence of a response much closer to a 100 percent response under such controlled conditions would seem to indicate that only a proportion of the fish were influenced by the orienting factor. If, for example, half of the fish were influenced by the testing factor and the other half entered the channels at random, the resulting ratio would be 3 : 1.

A possible sexual variation in the response of the fish was considered. A trap was placed at the head of each channel and after a series of CO_2 tests had been run, the fish in each trap were examined for sex. This procedure was later repeated with a series of temperature tests. The data (table 17) indicate that the sex of the fish has no effect upon its response to differences in CO_2 and temperature.

The possibility of individual variation in the sensitivity of the fish to temperature differences and to CO_2 differences was examined by gradually increasing the differences between the two channels. Had there been significant individual variation in sensitivity, the response would have become greater as the difference between channels gradually exceeded the thresholds of more and

TABLE 17.—*Influence of sex on the response to CO_2 and temperature*

Factor and sex	Number of decisions	Percent that entered channel with—			
		CO_2 content—		Temperature—	
		Higher	Lower	Higher	Lower
CO_2:					
Male	54	26	74	...	...
Female	70	27	73	...	...
Temperature:					
Male	24	...	...	79	21
Female	38	...	...	76	24

more fish. This, however, did not occur. The response remained approximately 3 : 1 even at the maximum attainable differences (>7.00 p. p. m. free CO_2 and 3.0° C.).

The possibility was also considered that some individuals might be completely insensible to the differences in temperature and CO_2 which were being used in the experiments. An experiment was set up in which fish that had previously been tested were again subjected to the same choice. A trap was placed at the head of each channel and a series of CO_2 tests were made. The trapped fish were then brought back to the entrance of the experimental trough and the CO_2 tests repeated. The data (table 18) show that the response of the fish that had previously entered the channel with the higher CO_2 was approximately 3 : 1 in favor of the channel with the lower CO_2, and those fish which had previously entered the channel with the lower CO_2 also exhibited a 3 : 1 response in favor of the channel with the lower CO_2.

Such evidence strongly suggests that the 3 : 1 ratio is not due to the failure of particular individuals or particular groups of individuals to respond to the orienting factor. It seems more probable that the explanation lies in the behavior patterns inherent in all the fish. If, for example, every fish responded to an orienting factor only half the time and acted at random the other half, the result would also be a 3 : 1 ratio. Further

TABLE 18.—*Retesting the response of fish to CO_2*

Fish from channel with	Number of decisions	Entered channel with—	
		Higher CO_2	Lower CO_2
		Percent	*Percent*
Lower CO_2	111	27	73
Higher CO_2	54	30	70

experiments may be necessary to throw some light on the nature of the ratio and to learn whether the phenomenon has any significance beyond the restricted circumstances of this experimental method.

DISCUSSION

When the results of the preceding experiments are compared with the findings of other investigators several interesting possibilities are suggested. One possibility is that the response of the fish to temperature differences might be a family characteristic. The two species of fish, *Pomolobus pseudoharengus* (Wilson) and *Pomolobus aestivalis* (Mitchill), which at Bournedale showed a consistent preference for warmer water, are members of the family Clupeidae. Shelford and Powers (1915) found that herring, *Clupea pallasi*, fry preferred warmer water. The observations of Roule (1933) indicated that migrating shad, *Paralosa nilotica rhodanensis* and *Alosa alosa*, which also belong to the family Clupeidae, selected water of higher temperature.

The threshold of the response to temperature differences shown by the two species of fish at Bournedale (0.5° C.) agrees very closely with that reported by Shelford and Powers (1915) for herring fry. This threshold may seem high compared to the minimum effective thermal stimulus range for certain fresh-water fishes (differences of 0.03° to 0.07° C.) reported by Bull (1936). However, it must be remembered that this temperature difference represents the minimum temperature difference which will provoke an unconditioned orientative response in the fish. The minimum temperature difference which can be perceived by the fish is probably much less.

Powers and Hickman (1928) presented evidence to show that rivers draining lakes usually had lower CO_2 tensions than other rivers (average difference 0.5 mm. Hg). Powers (1939) contended that by means of these differences in CO_2 tension migrating fish could select certain types of streams. The results of the CO_2 experiments at Bournedale would fit well into his argument. The alewife and the glut herring both showed a strong preference for water of lower CO_2 tension (threshold difference 0.1 mm. Hg). These fishes usually spawn in small ponds and shallow lakes and the choice of water of lower CO_2 content would result in the selection of streams leading to lakes or ponds.

The fundamental nature of the response of the fish to differences in CO_2 and to differences in temperature is indicated by the manner in which CO_2 and temperature were able to dominate competing orienting factors in the exploratory tests shown on page 390. The low threshold values for these responses also suggest their probable importance.

The experiments examining the orientative influence of *p*H (p. 388) confirm the conclusion of Powers (1930) that *p*H was largely ineffective as a factor influencing the behavior of aquatic animals. Whether the response of the fish in the experiments at Bournedale was to differences in free CO_2 or to the associated differences in HCO_3 was not actually established although the threshold values involved suggest that the response was to free CO_2. If the response was to the free CO_2 the influence of CO_2 differences is limited to waters with a *p*H of less than 8.4. This fact might be used to advantage in an experiment to determine to which of the two factors the fish are responding.

Although the main efforts of this investigation were directed toward examining the orientative influence of CO_2 and temperature upon the migrating fish, this was not meant to imply that these are the only major influences which might be concerned in other situations. The influence of differences in dissolved O_2 may be of great importance when lower O_2 values are concerned, which was not the case at Bournedale. Under special conditions flow characteristics such as velocity and turbulence may play an important part in directing the fish. The role of olfactory memory needs to be further explored. The influence of factors affecting the orientation of the fish indirectly (e. g., by controlling the depth of swimming) must be considered. It was largely to stress the fact that many factors may be concerned in fish orientation that the exploratory tests involving velocity, turbulence, and visual factors were included in this report.

Perhaps one of the most important considerations to which the foregoing experiments call attention is that not only are there many factors which may have a directional influence upon the migrating fish but also that they must all be considered together. The experiments examining

the relative influence of CO_2 and temperature demonstrated conditions under which the response to temperature differences could dominate the response to CO_2 differences when the factors were in opposition. The reverse situation was also demonstrated. The experiments further revealed circumstances under which the two factors were equal and the influence of the one balanced the influence of the other. Had an observer at these experiments been considering only temperature, for example, he would have seen the fish choose the warmer water in one group of tests and the colder water in another. During the third group of tests he would have concluded that the fish were indifferent to temperature. It is quite possible that many apparently contradictory observations may be explained in this way, e.g., the observations of Ward (1920), Chamberlain (1907), and Foerster (1929), regarding the influence of temperature on sockeye salmon.

One of the considerations that had to be taken into account during the experiments at Bournedale was that the fish might be reacting to a change in water conditions. This possibility became evident in one of the exploratory tests examining the influence of light intensities. One channel of the experimental trough was shaded and the other was left exposed to full sunlight. When the undivided lower portion of the experimental trough was shaded, the fish chose the shaded channel. When the lower part of the trough was exposed to sunlight, the fish chose the sunlit channel. Thus the fish showed no preference for either the sunlit or the shaded channel. They simply avoided any change in light conditions.

During experiments in which water was modified by the introduction of gaseous CO_2 the fish avoided the modified water. Although the fish entered the trough in a mixture of water from both channels (fig. 2), and before entering they had been subjected to a mixture of both waters in the upstream end of the retaining pool (fig. 4), the possibility that the reaction of the fish was one to change in chemical conditions still had to be considered. However, in one experiment which was made at Bournedale, the CO_2 content of the water of one channel was reduced by the addition of NaOH. In that experiment (see p. 388) the fish showed a preference for the modified water. It, therefore, seems improbable that the response of the fish in the other CO_2 experiments was a response to change in chemical conditions.

Powers and Clark (1943), discussing certain gradient-tank experiments with brook trout, *Salvelinus f. fontinalis*, and rainbow trout, *Salmo gairdneri iridus*, presented evidence indicating that the reactions of the trout to CO_2 in these experiments might be characterized as reaction to change. They made the observation that "The immediate response to carbon dioxide tension of the water depends to a large extent upon the carbon dioxide tension to which the fish is adjusted." The period of adjustment in their experiments was only 10 to 15 minutes.

If this observation were true for migrating fish then CO_2 would probably have little directive influence. The fish adjusted to the CO_2 tension of the sea would be restrained from entering fresh water with a different CO_2 tension. At a junction between two streams the fish would tend to select the stream with the larger volume in an effort to remain in the CO_2 tension nearest to the one to which it had become adjusted.

A possible explanation is suggested by an earlier statement of Powers (1939):

> The ova and sperm heads contain a protein (protamine) containing large percentages of arginine. It requires a vast protein metabolism to obtain the necessary arginine. Protein metabolism and especially fasting—both necessary for the liberation of arginine from the muscular tissue of the salmon—tends to produce acidosis of the blood, *i. e.*, lower the alkali reserve of the blood. This is common knowledge. A salmon with a low alkali reserve blood would find low carbon dioxide tension water more advantageous.

The special physiological state of the migrating fish might prevent it from becoming adjusted to its environment.

As experimental evidence is acquired indicating physical and chemical differences may have a directional influence upon migrating fish, the method by which the fish is oriented to these differences becomes an important consideration, particularly when one is trying to relate artificial experimental conditions to situations found in nature.

There are two methods by which fish might become oriented in a gradient. The fish might make a simultaneous comparison of intensities of stimu-

lation by means of symmetrically placed receptors and turn toward (or away from) the maximum stimulation. If this was the method of orientation, the orientative influence of gradients would be limited to those gradients great enough so that the differences between points a few inches apart (the distance between paired receptors) are above the threshold of sensory perception of fish. Gradients as high as this do actually exist in nature but usually only as a narrow zone between two bodies of water which are just beginning to mix.

A second method by which a fish might orient in a gradient is similar to the "trial" method of orientation characterized by Jennings (1906) as "selection from among the conditions produced by various movements." He points out that in this type of behavior, "Each stimulus causes as a rule not merely a single definite action that may be called a reflex, but a series of "trial" movements, of the most diverse character, and including at times practically all the movements of which the animal is capable." This type of orientation Fraenkel and Gunn (1940) have labeled "klinotaxis," and defined as "a directed orientation made possible by means of regular deviations and involving comparison of intensities at successive points in time," and they pointed out examples of such behavior in many invertebrates. In this method of orientation the fish, subjecting itself to varied conditions by its active movements, would select the most favorable condition or direction. The method involves both movement and comparison of intensities of stimulation that are successive in time.

The behavior of the fish as they selected a channel in the experimental trough at Bournedale strongly suggested that this latter method of orientation is the one used. As the fish entered the trough they usually swam from one side to the other, approaching first one channel and then the other. When once the fish had left the narrow zone in which the water was mixing (fig. 2) it was no longer subjected to a gradient. Its sensory receptors were all subjected to the same intensity of stimulation and, therefore, the current was the only orientative influence directing the movement of the fish upstream, unless memory was involved. Yet the fish repeatedly swam from one side of the trough to the other and frequently even after entering one channel, they turned back and entered the other.

Orientation by means of a comparison of intensities that are successive in time would make it possible for fish to become oriented in much smaller gradients than would be necessary if orientation was by a simultaneous comparison of intensities. The minimum gradient in which a fish could orient would depend on the speed of the fish and the time interval of its sensory memory.

The experiments at Bournedale have demonstrated that one group of migrating anadromous fishes will orient with reference to differences in certain physical and chemical water characteristics created artificially. It is logical to suppose that the fish will also be oriented by similar differences occurring along their migration routes in nature.

SUMMARY

The purpose of this investigation was to examine experimentally the influence of certain physical and chemical water characteristics upon the orientation of one type of migrating anadromous fish. The migrating fish were presented with a choice between two channels that carried water with different characteristics. The orientative influence of the water properties in question was measured by the number of fish selecting each channel. The reactions of more than 8,000 fish of the genus *Pomolobus*—alewife, *P. pseudoharengus* (Wilson), and glut herring, *P. aestivalis* (Mitchill)—were tested as the fish migrated upstream through the Herring River at Bournedale, Mass., toward their spawning area, in the springs of 1949 and 1950.

The fish were not removed from the stream or handled in any way. Each was tested individually and tested only once (the few exceptions are noted). The findings of this investigation were:

1. Presented with a choice of waters having different temperatures, 77 percent of the fish entered the channel with the warmer water when the temperature difference continuously exceeded 0.5° C. The temperature differences examined ranged from 0.4° to 3.0° C. Water temperatures during experiments varied from 11.1° to 22.3° C.

2. The response of the fish to temperature differences near the threshold difference decreased as the temperature level of the water increased.

3. Presented with a choice of waters having different amounts of free CO_2, 72 percent of the fish entered the channel with water of a lower

free CO_2 content when the free CO_2 difference exceeded 0.3 p. p. m. (0.1 mm. of Hg in terms of CO_2 tension). The differences in free CO_2 examined ranged from 0.2 p. p. m. CO_2 to greater than 4.0 p. p. m. The amount of free CO_2 in the water during these experiments varied from 0.8 p. p. m. to 7.1 p. p. m.

4. The sex of the fish appeared to have no influence on its response to differences in CO_2 content or in temperature.

5. Exploratory experiments indicated that visual factors and such factors as velocity and turbulence can influence orientation.

6. The fish did not respond to a difference of 1.1 p. m. m. O_2 created during experiments. The amount of O_2 in the water during the experiments ranged from 10.5 p. p. m. to 10.7 p. p. m. and water temperatures ranged from 15.4° to 19.1° C.

7. The fish were indifferent to *p*H differences as large as 0.8 *p*H unit when associated differences in free CO_2 were less than the threshold 0.3 p. p. m. The *p*H of the water varied from 6.5 to 7.3 during these experiments.

8. The relative orientative influence of CO_2 and temperature, when the two factors were in opposition, was shown to depend upon their relative differences of magnitude. A difference in temperature of approximately 2° C. dominated an opposing difference in free CO_2 of 2.0 p. p. m. A difference of CO_2 slightly in excess of 2.4 p. p. m. balanced the opposite effect of a 2° C. temperature difference. A difference of >7.0 p. p. m. CO_2 dominated over a temperature difference of 0.6° C.

9. The behavior of the fish during the experiments indicated that the orientation was accomplished by a method of "trial" involving both movement of the fish and a comparison of intensities of stimulations which were successive in time.

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FISHERY BULLETIN 58

UNITED STATES DEPARTMENT OF THE INTERIOR, Oscar L. Chapman, *Secretary*

FISH AND WILDLIFE SERVICE, Albert M. Day, *Director*

ABSTRACT

With the initiation of studies of the biology, ecology, and behavior of Pacific tunas by the Pacific Oceanic Fishery Investigations, U. S. Fish and Wildlife Service, in the Hawaiian Islands in 1948 the need for a current systematic compilation of scientific papers dealing with the biology of Pacific tunas became pressing. This bibliography was prepared for the use of the biologists and technicians working in the Investigations as well as for tuna researchers in general, and contains many references to Japanese research, the results of which have hitherto not been generally available outside Japan.

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